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Functional Relationships Between Salal Understory and Forest Overstory

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by D.J. Vales
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FUNCTIONAL RELATIONSHIPS BETWEEN SALAL UNDERSTORY AND FOREST OVERSTORY[a]

D.J. Vales[b]

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ABSTRACT

Abundance of salal (*Gaultheria shallon* Pursh) and its relationship to forest overstory were studied in immature forest stands on Vancouver Island having some topographical characteristics of deer winter ranges. Plots sampled over a range of stocking levels indicated that salal density was strongly related to single forest stand characteristics (r^2 = 0.92-0.94) but predictive equations differed between plant associations. Most equations predicting salal biomass or cover did not differ between plant associations. Equations calculated from data from single stands accounted for more of the variation in salal abundance (r^2 = 0.73-0.97) than equations developed from data from several stands (r^2 = 0.39-0.92). Mean salal shoot height was greatest under overstory cover of 65 to 80%.

Transmission of global, direct, diffuse, and diffuse photosynthetically active solar radiation through forest canopies was studied on 12 plots during sunny days in summer. The proportions of radiation transmitted were a function of forest stand characteristics and differed among radiation components. The relationship between the proportion of diffuse radiation transmitted and stand characteristics differed among stand structures. When direct beam radiation was scattered by open crowns of short trees and crowns extended below the height of radiation sensors, diffuse radiation below the canopy was higher than outside.

The extent to which different forest stand characteristics predict transmission and follow Beer's law were explored. Sum of tree diameters and Reineke's stand density index predict transmission of global (i^2 = 0.80-0.95) and direct radiation (i^2 = 0.70-0.98) best. Overstory cover predicts transmission of diffuse radiation best (i^2 = 0.74) where there is extensive inter-plot variation and bases of tree crowns are above sensors. Forest stand characteristics obtained by different sampling methods gave different predictabilities of the components transmitted.

Differences were found between hemispherical photograph estimates of diffuse radiation transmitted and measured transmission of diffuse and diffuse photosynthetically active radiation. Photographic estimates of direct radiation transmitted differed from measured transmission of direct radiation.

The relationships of salal characteristics to transmission of solar radiation components were examined. Salal density, basal area, foliar productivity, biomass, and cover all increased asymptotically with increasing transmission. The growth of salal was more closely related to transmission of direct radiation (i^2 = 0.65-0.99) than to global, diffuse, or diffuse photosynthetically active radiation. The rate at which salal abundance plateaued was fastest for transmission of direct radiation.

Salal shoot height and basal diameter were largest for low to moderate proportions of radiation transmitted. The lowest and greatest proportions transmitted seemed to adversely affect salal shoot height and diameter. Shoot productivity increased asymptotically with increased transmission. Salal maximum abundance and shoot size are regulated by the amount of direct solar radiation received at a site and probably by an interaction with a site's moisture regime.

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CHAPTER 1. GENERAL INTRODUCTION

Manipulating forest stands has been suggested as a technique to encourage forage production for wildlife and domestic stock (e.g., Young et al. 1967). To manage forest stands for forage it is important to know how changes in overstory affect the understory. Studies have examined the response of forage (understory) to manipulation of the forest canopy (overstory) and relationships have been drawn between the two (for review see Bartlett and Betters 1983). Understory vegetation also competes with trees for moisture (e.g., Tan et al. 1977) and likely nutrients (e.g., Weetman et al. 1986). Maintaining dense forest stands to shade out the understory can reduce this competition (Black et al. 1980; Black and Spittlehouse 1981).

Few researchers have studied potential factors regulating understory production (e.g., Anderson et al. 1969; Zavitkovski 1976), and these studies have had mixed results. Causal relationships between overstory and understory have often been considered as functions of transmission of solar radiation (e.g., Alaback 1982).

Objectives of this study are treated in separate chapters and are: 1) to examine the relationships of salal (*Gaultheria shallon* Pursh) density, foliar productivity, biomass, cover, and height to forest stand characteristics and to test for differences in the relationships among sites; 2) to study the relationships of transmission of global, direct, diffuse, and diffuse photosynthetically active solar radiation to forest stand characteristics; 3) to evaluate the extent to which salal abundance, growth and shoot size are related to transmission of solar radiation; and 4) to discuss the forest and wildlife management implications of these findings. Emphasis in this study is on forestry practices in untended, immature stands in the Coastal Western Hemlock Zone on Vancouver Island. The results from this study will supplement limited work previously done on understory-overstory relationships in clearcut, mature, and old-growth forests done by the Forestry-Wildlife Group at U.B.C.

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CHAPTER 2. RELATIONSHIPS BETWEEN SALAL UNDERSTORY AND FOREST OVERSTORY

INTRODUCTION

In the coastal forests of much of the Pacific Northwest salal (*Gaultheria shallon* Pursh) is an important understory component for two major reasons. It competes with commercial tree species for moisture (Tan et al. 1977; Price et al. 1986) and possibly nutrients (Weetman et al. 1986). Second, salal is a major winter forage for Columbian black-tailed deer (*Odocoileus hemionus columbianus* Richardson; Cowan 1945; Brown 1961; Crouch 1968; Jones 1975; Rochelle 1980). While foresters may want to maintain dense forest stands to reduce the abundance of salal (Black et al. 1980; Black and Spittlehouse 1981), wildlife managers are considering thinning regimes that might encourage salal forage abundance (Nyberg et al. 1986). In each case the relationships of salal growth and abundance to forest stand characteristics are critical. Other than the work of Long and Turner (1975), Stanek et al. (1979), Koch (1983), and Bunnell and Vales (1986), these relationships are not well documented nor are they tested for different plant associations.

This study examines the relationships between salal and forest stand characteristics. Specific objectives were to: 1) develop regressions predicting salal density, productivity, biomass, and cover from forest stand characteristics; 2) identify the forms of the relationships between salal variables and forest stand characteristics; 3) test for differences in the relationships among biogeoclimatic variants (Klinka et al. 1984) and between biogeoclimatic subzones (Krajina 1965) and plant associations (Orloci 1964, 1965); 4) identify the best forest stand characteristics to use for predicting salal abundance; and 5) examine the qualitative relationship of salal height to forest stand characteristics.

STUDY AREAS

Twenty-two plots were sampled on Vancouver Island and at the University of British Columbia Research Forest, UBCRF (Fig. 2.1). Ten plots were in the *Gaultheria* - Western Hemlock - Douglas-fir (G-WH-DF) plant association (Orloci 1964, 1965) in the Vancouver Island variant (CWHa$_1$; Klinka et al. 1984) of the Coastal Western Hemlock Dry Subzone (CWHa; Krajina 1965). Four plots also were sampled in the G-WH-DF plant association in the windward submontane variant of the Coastal Western Hemlock Wet Subzone (CWHb$_1$). These four plots were all on the same hillside in the same stand and were separated by less than 800 m. One UBCRF plot was located in the *Vaccinium* - *Gaultheria* - Western Hemlock - Douglas-fir (V-G-WH-DF) plant association (Orloci 1964, 1965) in the CWHb$_1$. This plot was combined with the Vancouver Island CWHb$_1$ plots for analyses because it had a similar soil moisture-nutrient regime (hygrotope-trophotope; Klinka 1976). Seven additional plots were sampled in the V-G-WH-DF plant association in the leeward submontane variant of the Coastal Western Hemlock Wet Subzone (CWHb$_3$). These seven CWHb$_3$ plots were all located on the same hillside, in the same stand, and were separated by less than 800 m.

All plots (except the UBCRF CWHb$_1$ plot in old growth) were in immature stands containing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Other tree species encountered were western redcedar (*Thuja plicata* Donn), amabilis fir (*Abies amabilis* (Dougl.) Forbes), yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), and western white pine (*Pinus monticola* Dougl.). Understory vegetation was predominantly salal with red huckleberry (*Vaccinium parvifolium* Smith) and Oregon grape (*Mahonia nervosa* Pursh) commonly present.

Soils were Humo-Ferric Podzols on morainal or colluvial veneer (Klinka et al. 1984). Of the soil characteristics examined, LFH and Ae layer development differed most among plots. Mor humus was poorly developed on most plots. Average annual precipitation is 2123 mm in the CWHa, 2682 mm in the CWHb$_1$, and CWHb$_3$ is between the two (Klinka et al. 1984). Hygrotope-trophotope combinations for the CWHa and CWHb$_3$ plots were moderately dry to slightly dry and nutrient poor to medium. CWHb$_1$ plots were slightly dry to fresh and nutrient poor to medium. Characteristics of plots are listed in Table 2.1.

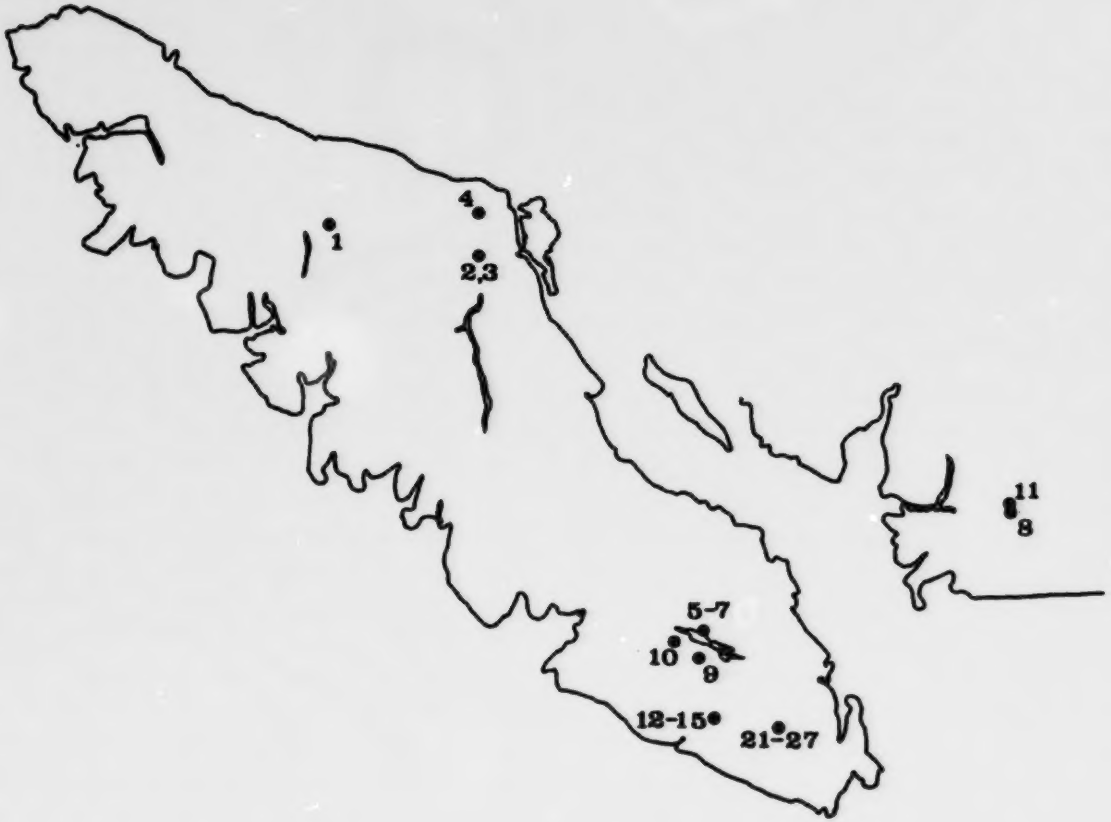

Figure 2.1. Plot locations on Vancouver Island and at the U.B.C. Research Forest.

TABLE 2.1 Descriptions of plots used to sample salal and forest stand characteristics

Plot	Location name	Latitude-Longitude	Subzone-variant	Plant assoc.	Aspect (°)	Elev. (m)	Slope (%)	Age	MCC[a]	NTREES[b] (#/ha)	BA[b] (m²/ha)	Avg. DBH[b] (mm)	Avg. Ht.[b] (m)	Site[c] index
1	Woss	50° 12′ - 126° 28′	CWHa	G-WH-DF	230	430	30	28	0.91	2533	37.7	131	12.4	36.4
2	Brewster 1	50° 07′ - 125° 39′	CWHa	G-WH-DF	215	270	15	37	0.78	1600	46.7	173	13.6	38.4
3	Brewster 2	50° 07′ - 125° 39′	CWHa	G-WH-DF	220	260	55	36	0.55	533	21.2	213	13.6	32.2
4	Mcreight	50° 15′ - 125° 37′	CWHa	G-WH-DF	218	150	48	53	0.79	1778	53.4	178	16.1	29.5
5	Youbou 1	48° 54′ - 124° 18′	CWHa	G-WH-DF	206	310	52	60	0.64	756	35.0	235	25.2	42.9
6	Youbou 2	48° 54′ - 124° 18′	CWHa	G-WH-DF	215	310	45	59	0.78	1733	34.4	145	15.6	35.3
7	Youbou 3	48° 54′ - 124° 18′	CWHa	G-WH-DF	173	200	8	34	0.35	267	14.8	219	15.7	36.5
8	UBCRF M-G	49° 17′ - 122° 28′	CWHa	G-WH-DF	115	375	10	44	0.65	667	30.7	222	18.1	40.4[d]
9	Gordon R.	48° 49′ - 124° 19′	CWHa	G-WH-DF	261	630	43	42	0.90	2711	54.9	149	15.0	36.0
10	Raymond Cr.	48° 52′ - 124° 28′	CWHa	G-WH-DF	210	390	60	39	0.75	1200	32.5	165	15.5	39.7
11	UBCRF V-G	49° 17′ - 122° 28′	CWHb$_1$	V-G-WH-DF	237	590	25	150+	0.90	1244	61.0	210	15.6	30.0
12	Harris Cr 1	48° 37′ - 124° 15′	CWHb$_1$	G-WH-DF	215	210	50	49	0.64	844	25.5	179	12.8	26.5
13	Harris Cr 2	48° 37′ - 124° 15′	CWHb$_1$	G-WH-DF	221	200	40	50	0.80	2000	62.2	185	17.6	36.5
14	Harris Cr 3	48° 37′ - 124° 15′	CWHb$_1$	G-WH-DF	232	200	50	48	0.84	2444	67.6	171	17.4	35.0
15	Harris Cr 4	48° 37′ - 124° 15′	CWHb$_1$	G-WH-DF	204	210	48	49	0.79	2089	62.0	182	13.9	27.9
21	Weeks L. 1	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	240	570	30	30	0.58	889	10.1	110	9.7	37.8
22	Weeks L. 2	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	240	570	30	30	0.42	756	8.5	118	10.3	37.0
23	Weeks L. 3	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	220	570	20	30	0.81	2222	41.6	144	13.4	37.8
24	Weeks L. 4	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	220	570	20	30	0.64	1111	26.1	159	14.3	41.0
25	Weeks L. 5	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	220	570	23	30	0.74	1200	20.0	138	13.6	41.4
26	Weeks L. 6	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	219	550	19	30	0.90	2622	38.9	128	12.7	37.0
27	Weeks L. 7	48° 36′ - 123° 52′	CWHb$_1$	V-G-WH-DF	214	600	22	30	0.76	1378	17.5	119	11.5	37.7

[a] Mean crown completeness estimate of forest overstory cover.

[b] Derived from measurement of all trees ≥ 8.0 cm within the plot.

[c] 100 year Douglas-fir reference based on total age.

[d] For western hemlock at 100 years total age.

METHODS

Plots were selected to encompass a range of overstory cover and to have topographic characteristics similar to deer winter ranges (sensu Jones and Bunnell 1984). Selectively locating plots is less time consuming than randomly locating plots and avoids heterogeneous sites, transitions, and ecotones (Kojima and Krajina 1975). Although deer winter ranges are typically located in old-growth forests, young forests managed as black-tailed deer winter ranges may serve as replacements for old-growth winter ranges in the future (Nyberg et al. 1986). Criteria used to select plots were: stand immaturity and homogeneity of forest canopy structure and salal cover, stand ages 30-60 years, overstory cover 35-95%, no thinning, no fertilization, no deciduous trees, slopes 10-60%, aspect 200-245°, and elevation 200-700 m.

Understory

Plots 9 x 25 m (0.0225 ha) were laid out with the long edge para lel to slope contours. Salal was sampled in 13 - 0.5 x 0.5 m (0.25 m^2) quadrats systematically located along each of four equi-spaced transects (n = 52/plot).

Because of salal's complex, clonal growth form (Koch 1983), individual plants were difficult to distinguish and therefore a salal shoot was considered as the basic sample unit. A shoot was defined as any stem emerging from the litter layer that had roots. In the field it was often difficult to distinguish shoots from non-rooted stems; two stems often emerged from the ground next to each other, and when one stem was pulled to determine height, other stems were sometimes found to be connected to it just below the litter or humus layer. Several stems that did not have roots and were connected to a main rhizome were considered as one shoot. Shoots with roots could obtain water and nutrients and be somewhat independent of the rest of the plant.

Within each quadrat, percent cover of salal foliage, excluding the current season's growth (to avoid errors among plots associated with date of sampling), was visually estimated. All rooted salal shoots were measured for basal diameter (point above roots and litter surface), natural repose height (vertical distance from point of rooting to intersection with a horizontal line drawn from uppermost portion of previous season's twig growth), "stretch" height (vertical distance from point of rooting to uppermost part of previous season's twig growth when the shoot was pulled upright), and current growing season's leaves on all shoots in the quadrat were counted. Random samples of at least 30 salal shoots that encompassed a range of shoot sizes in each of ten plots were clipped, oven-dried, and weighed to develop allometric equations predicting foliar and total shoot biomass (Vales et al. in prep.). Standing crop foliar and total biomass estimates were derived from the allometric equations and excluded current annual growth biomass. Current annual growth (CAG) leaves were randomly sampled from each plot (except for plot 11 in which plot 8 leaf biomass was used) in the fall after completion of the season's growth, oven-dried at 65°C for 24 hours and weighed to the nearest 1 mg to determine average leaf biomass. CAG foliar biomass was derived by multiplying average leaf biomass by number of CAG leaves per quadrat.

Overstory

Forest overstory cover has been measured in a variety of ways (for review see Vales and Bunnell 1985) and many terms are used to define the proportion of sky covered by canopy. I use "mean crown completeness" (MCC) sensu Bunnell et al. (1985:181). MCC of each plot was measured with a moosehorn (Robinson 1947; Bonnor 1967) at the center of each quadrat ($n = 52$/plot). Stand age was obtained by boring at breast height (1.3 m) four dominant trees in the plot or nearby (less than 15 m from a plot edge) and adding the age corrections from Watts (1983:402). Site index was calculated for the four dominant trees bored using the equations from Watts (1983:424). Tree species were recorded and diameter at breast height (DBH), top height, and height to base of live crown (HBLC; height where the lowest live branches were attached to the bole) were measured for all trees $>$ 8.0 cm DBH inside the plot. Trees $<$ 8.0 cm DBH and $>$ 20 cm tall were counted. Point samples were taken with a four basal area factor (BAF_4) prism at the four plot corners and plot center; species and DBH of "in" trees were recorded.

Definition of Variables

All understory measurements of density, biomass, and cover are reported as plot averages derived from 52 0.25-m^2 quadrats. Measurements of salal height are reported as plot averages of all shoots sampled.

DENSITY - average density of salal shoots.m^{-2}
CAGBIOM - average CAG foliar biomass of salal ($g \cdot m^{-2}$)
FOLBIOM - average foliar biomass of salal ($g \cdot m^{-2}$; excludes CAGBIOM)
TOTBIOM - average foliar+stem biomass of salal ($g \cdot m^{-2}$; excludes CAGBIOM)
PCTCOVER - average quadrat percent cover of salal
REPHT - average repose height of salal shoots (cm)
STRHT - average stretch height of salal shoots (cm)
MCC - mean crown completeness of plot (average of 52 moosehorn samples and reported as a fraction)
NTREES - number of plot trees.ha^{-1} $>$ 8.0 cm
BA - basal area ($m^2 \cdot ha^{-1}$) of plot trees $>$ 8.0 cm
AVGDIA - average DBH (mm) of plot trees $>$ 8.0 cm
SUMDIA - sum of DBH (mm/225 m^2) of plot trees $>$ 8.0 cm
HT - average tree height (m) of plot trees $>$ 8.0 cm
CRNDEP - average crown depth (HT - HBLC) of plot trees $>$ 8.0 cm
BAFBA - average stand basal area ($m^2 \cdot ha^{-1}$) of trees $>$ 8.0 cm determined from 5 BAF_4 prism samples
BAFDIA - average DBH (mm) of trees $>$ 8.0 cm sampled by 5 BAF_4 prism samples
BAFTREES - average number of trees$\cdot ha^{-1}$ $>$ 8.0 cm determined from 5 BAF_4 prism samples
BAFBADIA - DBH (mm) of tree of average basal area determined from prism samples
BAFSDI - Reineke's (1933) "stand density index" determined from prism sampling computed from $BAFTREES \cdot (BAFBADIA/25)^{1.6}$ (Long 1985)

Analyses

Salal quadrat samples and shoot measurements were tested for normality within plots (coefficient of skewness g_1 not significant, Sokal and Rohlf 1981:174) and homogeneity of variance among plots (Fox and Guire 1976:68). Transformations were necessary for all salal variables. A suitable transformation to normalize the data for one plot was not necessarily the best transformation for other plots. I used a single transformation for all plots which gave the largest number of plots having g_1 not significant ($p > 0.05$; minimum 14 of 22 plots). Transformations used were square root for quadrat density, cover, and shoot height; and cube root for all quadrat biomass estimates. Means and confidence intervals are reported backtransformed and quadrat means are multiplied by 4 to represent 1 m^2.

The backtransformed mean of each salal variable was regressed against single and multiple independent variables using forward selection, backward selection (MIDAS, Fox and Guire 1976), and all possible subsets regression (BMDP 9R, Dixon 1983). Backtransformed means were used rather than the transformed means because regression estimates obtained from equations based on backtransformed means were usually lower and provided a more conservative estimate of salal abundance. Best regressions were those having the lowest standard error of the estimate ($s_{y.x}$) and no trend in the residuals. Regressions were developed on untransformed, log, or reciprocally transformed independent variables. A reciprocal transformation usually gave a better equation than a log transformation for most equations and independent variables. For consistency here, curvilinear regressions have the independent variables reciprocally transformed. There seems to be no consistent curvilinear form of regression for published equations (see reviews in Bartlett and Betters 1983). Equations based on a reciprocal transformation of the independent variable give unrealistic estimates near zero. The results reported are the best for this data set and are applicable only within the range of the data. Because equations are developed on plot means, regressions are illustrated with 95% confidence intervals around plot means to show variability of salal samples. Reported $s_{y.x}$'s based on regressions of plot means may underestimate the true population variation.

Tests of equal regression slopes and intercepts were computed with analyses of covariance using the UBC SLTEST program (Le 1971). Except where otherwise stated, all statistical tests were at a = 0.05.

RESULTS

Regressions Predicting Salal Abundances

Simple linear regressions predicting estimates of salal abundances are given in Table 2.2. Equations are presented for MCC and the best independent variables derived from plot tree measurements and prism samples. This format permits examination of relationships based on overstory cover, factors operating within the plot, and factors possibly affecting salal from outside the plot (prism samples). Regressions based on plot tree measurements and prism samples also demonstrate the influence of sample design on accuracy of prediction ($s_{y.x}$). Equations are presented separately in the CWHa and $CWHb_3$ to show variability (r^2) across stands of different ages and locations (CWHa) compared to variability within a stand ($CWHb_3$). Regressions in the $CWHb_1$ only are excluded due to low sample size and narrow ranges of independent variables. Equations in the CWHa were always more variable than those in the $CWHb_3$ (Table 2.2; CWHa density versus MCC $r^2 = 0.93$). Multiple regressions used the same approach (Table 2.3). Variables representing the midstory, tree height, live crown ratio (CRNDEP/HT), species composition and site index were poor independent variables when used singly and were not consistently selected for inclusion in multiple regressions.

Form of Relationships

The relationships between salal density and forest variables were curvilinear and suggested that hyperbolic (1/X) or logarithmic (ln(X)) equations could be used. For equations where ln(X) gave the best predictability (smallest $s_{y.x}$), differences between reciprocal and logarithmic equations were small, but where 1/X gave the best predictability, differences were large. Because the 1/X was often better, I used a hyperbola to describe the relationship between salal density and stand characteristics for the range of these data.

Salal CAGBIOM was also hyperbolically related to stand characteristics (Table 2.2), with the 1/X transformation giving consistently better equations than an ln(X) transformation. Salal standing crop biomass was consistently hyperbolically related to stand characteristics in the CWHa and also for most combined data equations except when BAFSDI was used to predict TOTBIOM (Table 2.2). FOLBIOM and TOTBIOM, however, were linearly related to stand characteristics in the $CWHb_3$. Ranges of independent variables in the $CWHb_3$ were narrower than in the CWHa and may have affected the best form of the regression. As well, plots 21 and 27 had biomass estimates considerably higher than predicted and likely contributed to the linear form. The forms of the relationships predicting PCTCOVER were mostly linear, except for cover predicted by BAFSDI in the CWHa (Table 2.2).

TABLE 2.2 Simple linear regression equations of salal variables as a function of MCC, plot, and prism variables. Sample sizes: CWHa=10, CWHb$_1$=5, CWHb$_3$=7. Equations significant at $p \le 0.05$. Regression equation: $Y = b_0 + b_1X$

Y	Variant	X	b_0	b_1	r^2	$s_{y \cdot x}$
DENSITY:	CWHa+b$_1$	1/MCC[a]	-36.894	37.675	0.92	5.23
		1/SUMDIA	N.S.[b]	82571	0.86	7.30
		1/BAFSDI	-26.456	35631	0.73	9.50
	CWHb$_3$	1/MCC	-119.04	113.02	0.94	14.26
		1/SUMDIA	-45.059	344340	0.92	15.56
		1/BAFSDI	-43.481	45998	0.97	9.87
CAGBIOM:	CWHa	1/MCC	-33.804	32.681	0.78	9.95
		1/SUMDIA	N.S.	68511	0.72	11.25
		1/BAFSDI	-35.439	38345	0.73	10.89
	CWHb$_3$	1/MCC	-48.568	44.568	0.95	4.74
		1/SUMDIA	-18.752	133040	0.91	6.67
		1/BAFSDI	-18.386	17887	0.96	4.12
	All 3	1/MCC	-38.575	36.867	0.82	7.71
		1/SUMDIA	-8.5865	96966	0.75	9.09
		1/BAFSDI	-11.475	17861	0.65	10.90
FOLBIOM:	CWHa	1/MCC	-84.614	84.140	0.66	33.89
		1/SUMDIA	N.S.	182100	0.61	35.58
		1/BAFSDI	-93.610	102310	0.67	33.50
	CWHb$_3$	MCC	230.66	-227.48	0.73	24.34
		SUMDIA	152.36	-0.01817	0.89	15.84
		BAFSDI	179.74	-0.18985	0.88	16.51
	All 3	1/MCC	-79.705	86.729	0.62	30.49
		1/SUMDIA	N.S.	206830	0.66	29.04
		1/BAFSDI	N.S.	34535	0.58	32.90
TOTBIOM:	CWHa	1/MCC	-295.55	305.25	0.61	137.54
		1/SUMDIA	N.S.	690550	0.57	139.57
		1/BAFSDI	-337.95	378460	0.64	131.78
	CWHb$_3$	MCC	550.13	-547.89	0.76	55.28
		SUMDIA	358.32	-0.04302	0.88	38.19
		BAFSDI	426.24	-0.45503	0.89	36.20
	All 3	1/MCC	-258.12	279.06	0.61	100.33
		1/SUMDIA	N.S.	653580	0.61	100.23
		BAFSDI	409.15	-0.32395	0.43	121.79
PCTCOVER:	CWHa	MCC	76.344	-73.637	0.42	15.72
		SUMDIA	51.230	-0.00531	0.44	15.47
		1/BAFSDI	N.S.	18850	0.39	15.69
	CWHb$_3$	MCC	100.65	-104.47	0.86	7.52
		SUMDIA	61.623	-0.00764	0.87	7.20
		BAFSDI	74.591	-0.08241	0.92	5.73
	All 3	MCC	90.468	-91.103	0.58	12.18
		SUMDIA	51.695	-0.00509	0.48	13.53
		BAFSDI	56.308	-0.03968	0.48	13.58

[a] Prefix 1/ refers to the reciprocal of the independent variable.

[b] Coefficient not significant ($p > 0.10$).

TABLE 2.3 Multiple regression equations of salal variables as a function of MCC, plot, and prism variables. Equations significant at $p \le 0.05$. Sample sizes: $CWHa=10$, $CWHb_1=5$, $CWHb_2=7$

Y	Variant	Equation[a]	R^2	$s_{y\cdot x}$
DENSITY:	CWHa+b₁	N.S.[b]		
	CWHb₂	-82.347 + 63.436·1/MCC + 668.57·1/BA	0.98	8.71
		1465.4·1/BA - 4201.2·1/AVGDIA	0.94	13.88
		-179.46 + 123480·1/BAFTREES + 23213·1/BAFDIA	0.99	6.06
CAGBIOM:	CWHa	-79.352 + 41.170·1/MCC + 294.32·1/CRNDEP	0.93	5.75
		-54.619 + 117970·1/SUMDIA + 353.17·1/CRNDEP	0.93	5.76
		-66.310 + 44369·1/BAFSDI + 205.64·1/CRNDEP	0.82	9.63
	CWHb₂	131.93 - 118.73·MCC - 2.9369·CRNDEP	0.99	2.67
		572.35·1/BA - 1849.6·1/AVGDIA	0.93	5.96
		-68.507 + 50383·1/BAFTREES + 8212.3·1/BAFDIA	0.99	2.10
	All 3	-84.391+42.452·1/MCC+1951.1·1/AVGDIA+232.24·1/CRNDEP	0.93	5.12
		-43.995 + 115790·1/SUMDIA + 281.23·1/CRNDEP	0.86	6.94
		22224·1/BAFSDI - 4020.7·1/BAFDIA	0.73	9.50
FOLBIOM:	CWHa	-246.51 + 114.31·1/MCC + 1046.1·1/CRNDEP	0.92	17.39
		-179.14 + 329570·1/SUMDIA + 1216.5·1/CRNDEP	0.93	16.09
		-216.45 + 126273·1/BAFSDI + 818.26·1/CRNDEP	0.85	24.58
	CWHb₂	N.S.		
		244.52 - 0.05682·NTREES - 8.550·CRNDEP	0.93	14.01
		321.68 - 0.08421·BAFTREES - 12.828·CRNDEP	0.96	11.14
	All 3	-225.16+101.00·1/MCC+10960·1/AVGDIA+509.98·1/CRNDEP	0.78	24.43
		-147.03+291140·1/SUMDIA+7868.3·1/AVGDIA+666.39·1/CRNDEP	0.81	22.63
		N.S.		
TOTBIOM:	CWHa	-947.04 + 426.67·1/MCC + 4209.7·1/CRNDEP	0.91	72.48
		-701.56 + 123930·1/SUMDIA + 4877.7·1/CRNDEP	0.93	62.39
		-848.24 + 478028·1/BAFSDI + 3399.3·1/CRNDEP	0.85	90.23
	CWHb₂	N.S.		
		582.34 - 0.13432·NTREES - 20.838·CRNDEP	0.93	33.63
		768.28 - 0.20079·BAFTREES - 31.062·CRNDEP	0.97	22.11
	All 3	-629.72 + 335.85·1/MCC + 2638.4·1/CRNDEP	0.74	83.58
		-433.45 + 976490·1/SUMDIA + 3130.3·1/CRNDEP	0.79	76.06
		N.S.		
PCTCOVER	CWHa	159.61 - 120.64·MCC - 5.1860·CRNDEP	0.69	12.17
		129.50 - 0.009344·SUMDIA - 5.9870·CRNDEP	0.78	10.34
		1287.6·1/BAFBA - 12450·1/BAFDIA + 336.98·1/CRNDEP	0.82	9.44
	CWHb₂	N.S.		
		N.S.		
		120.73 - 0.03623·BAFTREES - 4.1137·CRNDEP	0.93	5.85
	All 3	143.24 - 114.22·MCC - 3.7744·CRNDEP	0.71	10.31
		120.81-0.02483·NTREES-0.14819·AVGDIA-3.6317·CRNDEP	0.66	11.49
		116.16-0.02646·BAFTREES-0.11013·BAFDIA-3.0284·CRNDEP	0.67	11.38

[a] Prefix 1/ refers to the reciprocal of the independent variable.

[b] Slopes of additional variables not significantly different from zero ($p > 0.10$).

Differences Among Relationships

Subzone effects within a plant association (G-WH-DF CWHa against G-WH-DF $CWHb_1$) and plant association effects within (G-WH-DF $CWHb_1$ against V-G-WH-DF $CWHb_3$) and across (G-WH-DF CWHa against V-G-WH-DF $CWHb_3$) subzones were tested. Results of slope tests differed with the independent variable. Equations predicting salal density as a function of reciprocally (1/X) transformed MCC, SUMDIA, NTREES, plot SDI, and prism BAFTREES were significantly different among the three variants (CWHa, $CWHb_1$, $CWHb_3$), but did not differ between the CWHa and $CWHb_1$ variants in the same plant association, indicating no subzone effect. $CWHb_1$ and $CWHb_3$ equations differed (plot 22 was dropped from the slope test to have ranges of independent variables nearly equal), indicating a difference between plant associations. Equations predicting salal density from reciprocal forms of BA, BAFSDI, and BAFBA, however, did not differ among variants.

No significant differences among variants were found for equations predicting CAGBIOM from 1/MCC, 1/SUMDIA, 1/SDI, 1/BA, and 1/BAFTREES. Equations differed significantly, however, with 1/NTREES, 1/BAFSDI, and 1/BAFBA as independent variables. Because forms of relationships for TOTBIOM and FOLBIOM differed between the CWHa and $CWHb_3$ (Table 2.2), covariance analysis to test for equation differences is not strictly valid. Acknowledging this, I still tested the regressions among variants using both untransformed and reciprocally transformed independent variables to explore potential differences. Equations did not differ using 1/MCC, 1/SUMDIA, 1/SDI, and 1/BAFTREES; hyperbolic equations with 1/BAFSKI and 1/BAFBA did differ. Equations did not differ among variants for all untransformed independent variables. Tests of equations with 1/NTREES indicated a difference among variants when predicting FOLBIOM, and 1/BA a difference among equations predicting TOTBIOM. Because there is some consistency of the results using the two different regression forms, equations are likely not different. The considerable variability of FOLBIOM and TOTBIOM equations resulted in high residual variance and thus the F-test was not significant. Equations predicting PCTCOVER did not differ significantly with any independent variable.

All slope tests were at a = 0.05. Had a been set to 0.01, all equations except 1/BAFSDI and 1/BAFBA predicting TOTBIOM would have indicated no significant difference among variants for equations predicting CAGBIOM, FOLBIOM, and TOTBIOM.

Reciprocally transformed BAFBA and BAFSDI gave slope test results opposite those of transformed MCC, SUMDIA, SDI, and BAFTREES for salal density and biomass relationships. Because 1/BAFSDI is a poorer predictor of density than plot samples of 1/MCC, 1/SUMDIA, 1/SDI, and 1/NTREES in the $CWHa{+}b_1$ (Table 2.2 in part), density relationships between the plant associations are likely different. Results were consistent among all untransformed independent variables for FOLBIOM and TOTBIOM. Results of slope tests using plot 1/SDI and 1/BAFSDI to predict salal density and biomass differed, but paired t-tests between SDI and BAFSDI within and across variants found no differences. Equations predicting salal biomass within variants were always slightly better using BAFSDI than SDI (r^2 differences between 0.01 and 0.10).

Differences among plots between plot measurements and prism samples were not consistent because plots were sometimes located in patches of dense or open stands. Plots located in stand gaps had an SDI less than that of BAFSDI (e.g., plots 3, 7, 10) and plots in dense patches had a higher SDI (e.g., plots 1, 2, 4, 13, 15, 23, 26). The equivocal slope tests may result from the way that prism samples accounted for the pattern of variation of plots being dissimilar from the surrounding stands.

Ranges of independent variables differed between plot tree measurements and prism samples (see Appendices 1 and 24). The range of SDI and BAFSDI, and BA and BAFBA were similar in the CWHa, but prism samples had a narrower range than plot measurements in the $CWHb_3$. The minima in the $CWHb_3$ plot samples of SDI and BA were closer to the minima in the CWHa, but minima for prism samples of BAFSDI and BAFBA diverged more (e.g., minimum SDI 295 in CWHa, 233 in $CWHb_3$; minimum BAFSDI 428 in CWHa and 238 in $CWHb_3$). Maxima followed the same pattern with maxima more different with prism samples than with plot measurements (maximum SDI 1335 in CWHa, 1028 in $CWHb_3$; maximum BAFSDI 1461 in CWHa, 818 in $CWHb_3$). Ranges overlapped more for measurements of plot trees (max-min SDI 733, BA 26.8) than for prism samples (BAFSDI 390, BAFBA 12.8). Discrepancies between the two sampling methods were less pronounced for number of trees. Reciprocal transformations accentuated the differences between ranges of values derived by the two sampling methods and likely contributed to the equivocal results.

Relative Predictability Among Independent Variables

Overstory cover (MCC) generally was a good independent variable predicting salal abundances (Table 2.2). Relationships of salal to MCC as a percent are illustrated in Figs. 2.2-2.6. SUMDIA was the best independent variable derived from measurements of plot trees for predicting salal. Equations based on plot basal area, number of trees, or SDI were not as good as using plot SUMDIA. SDI derived from prism samples was a better independent variable than prism samples of basal area or number of trees.

There were only modest differences in the $s_{y.x}$'s of each salal variable among independent variables in separate variants except for FOLBIOM and TOTBIOM predicted by MCC in the $CWHb_3$ and density predicted by BAFSDI (Table 2.2). MCC was a poorer predictor of FOLBIOM and TOTBIOM than other forest measurements in the $CWHb_3$, although MCC was good for combined data. BAFSDI was a poorer predictor of density in the $CWHa+b_1$ with considerable inter-plot variation of tree size and spacing. Other salal variables were predicted well by BAFSDI in the CWHa. In the $CWHb_3$ where trees were of relatively the same size, BAFSDI predicted all salal variables well. The poorest independent variable for combined data equations was BAFSDI because equations were found to differ among variants. Both sampling methods for stand characteristics accounted for nearly equal variation in individual variants, although the two methods often yielded different results for tests of equal equations among variants.

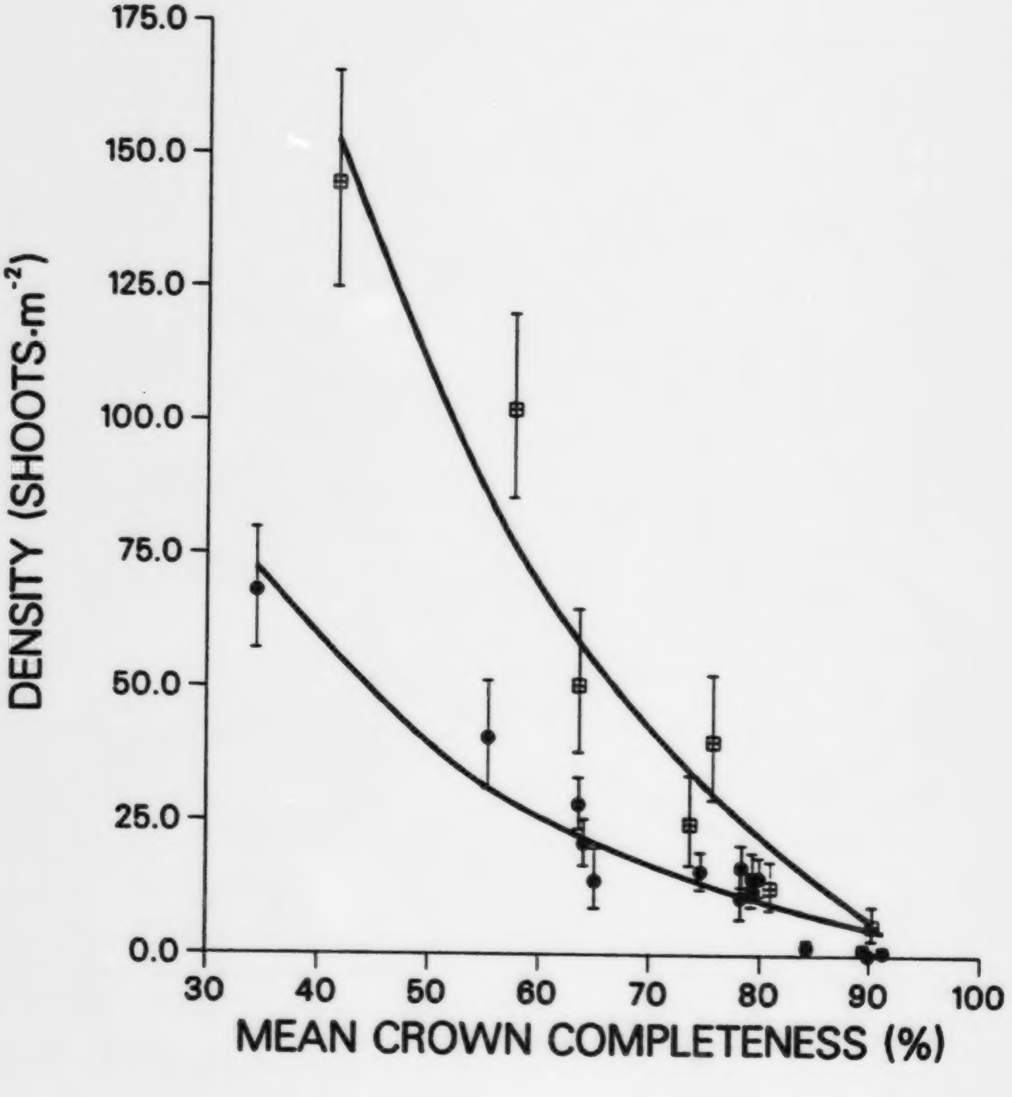

Figure 2.2. The relationship of salal density·m^{-2} and 95% confidence intervals to mean crown completeness. Lower equation is for CWHa and CWHb$_1$ combined data (•), upper equation CWHb$_3$ (⊞).

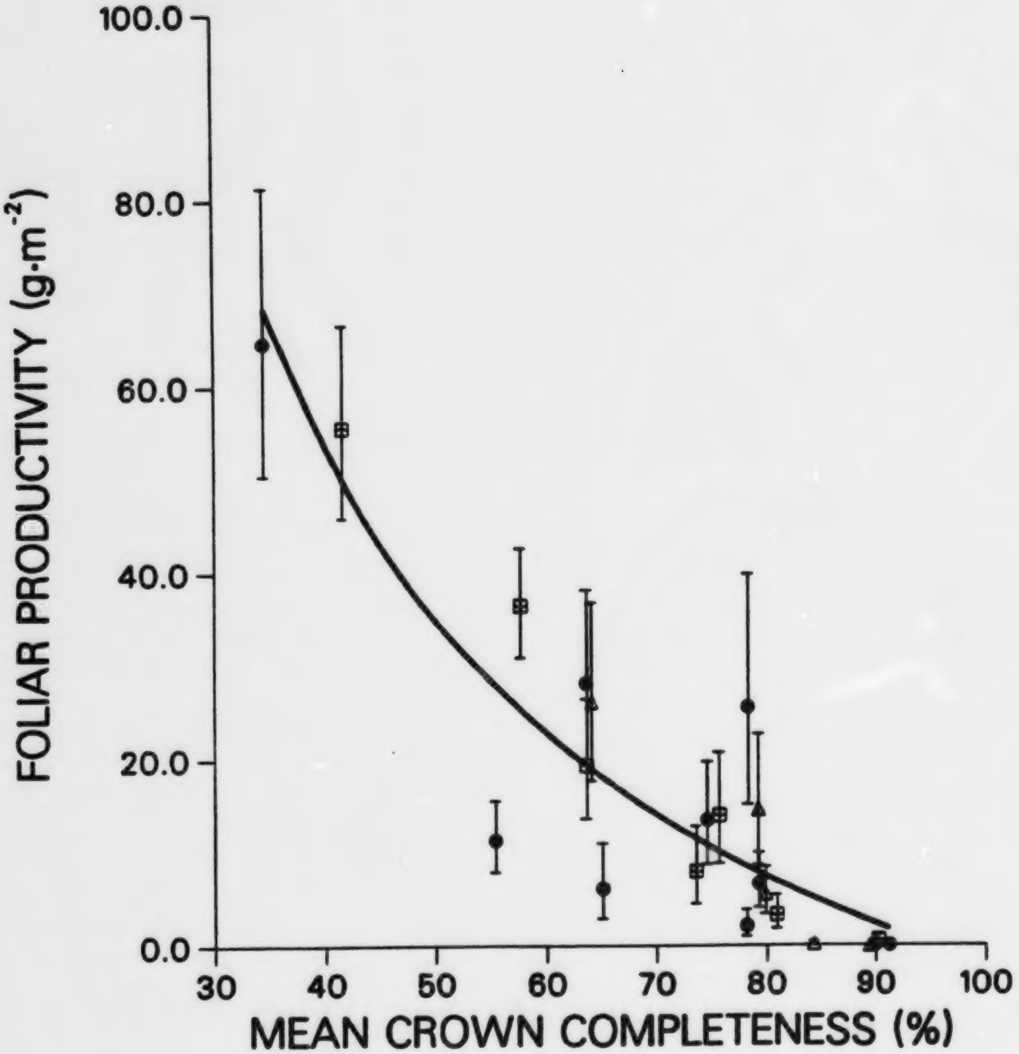

Figure 2.3. The relationship of foliar productivity ($g \cdot m^{-2}$; CAGBIOM) and 95% confidence intervals to mean crown completeness. CWHa (●), $CWHb_1$ (△), $CWHb_3$ (⊞). Equation is for combined data.

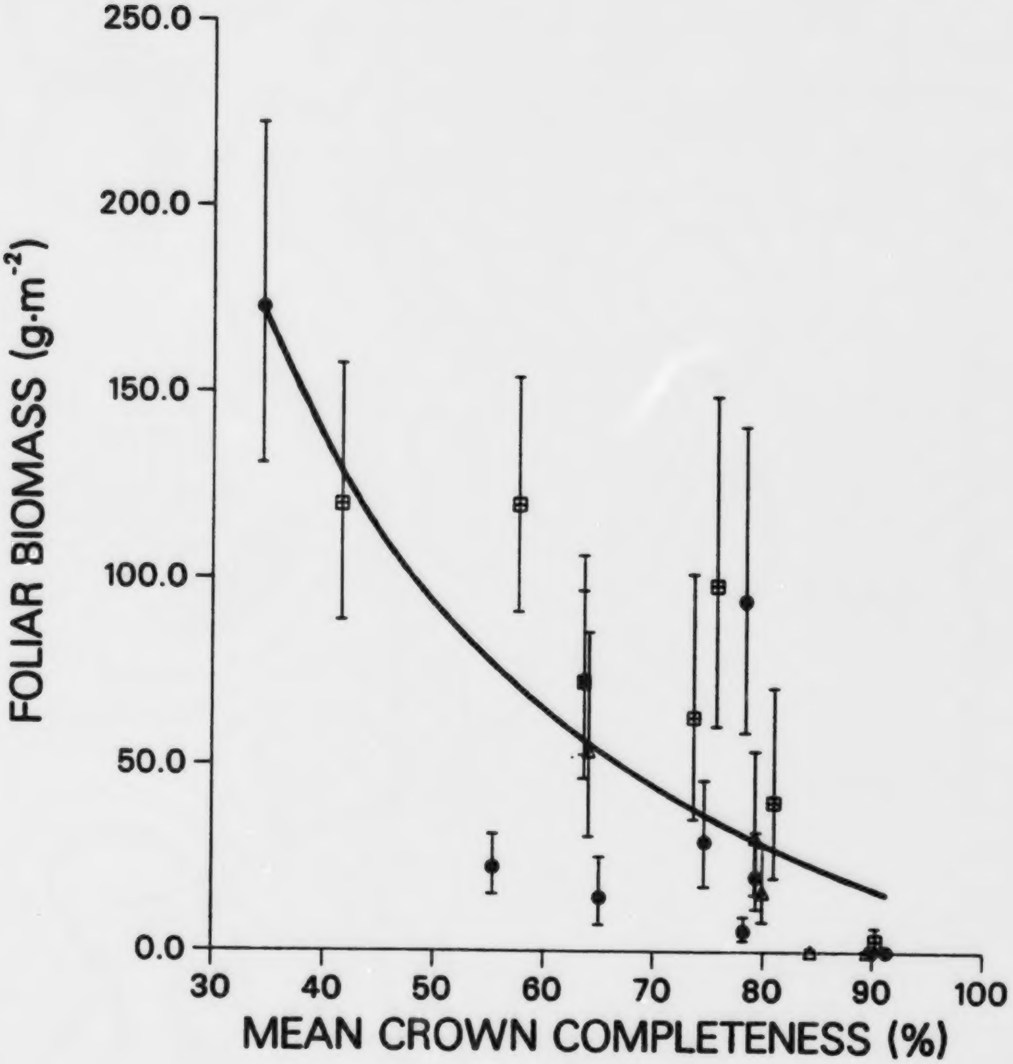

Figure 2.4. The relationship of salal foliar biomass ($g \cdot m^{-2}$; FOLBIOM) and 95% confidence intervals to mean crown completeness. CWHa (●), $CWHb_1$ (△), $CWHb_3$ (⊞). Equation represents combined data.

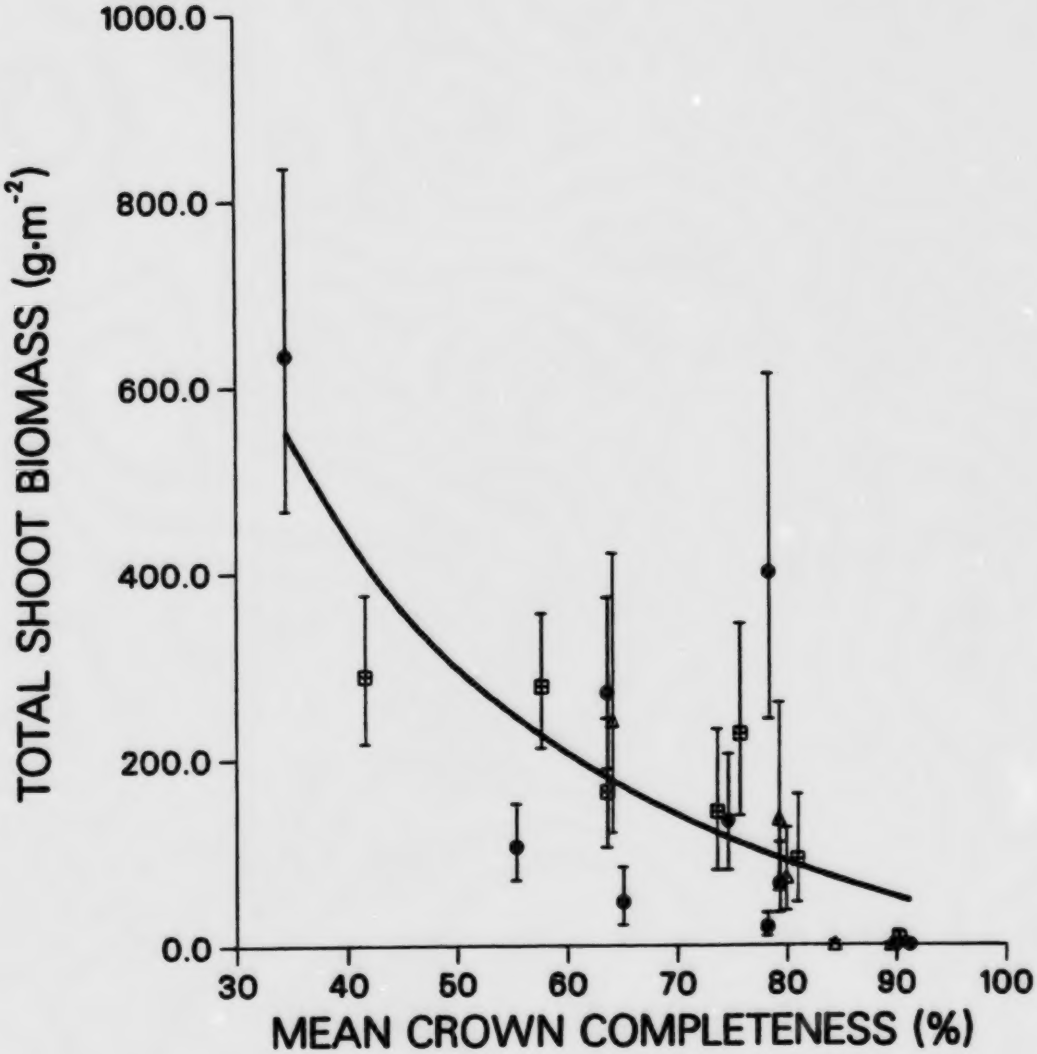

Figure 2.5. The relationship of salal total biomass ($g \cdot m^{-2}$; TOTBIOM) and 95% confidence intervals to mean crown completeness. CWHa (•), $CWHb_1$ (△), $CWHb_3$ (⊞). Equation represents combined data.

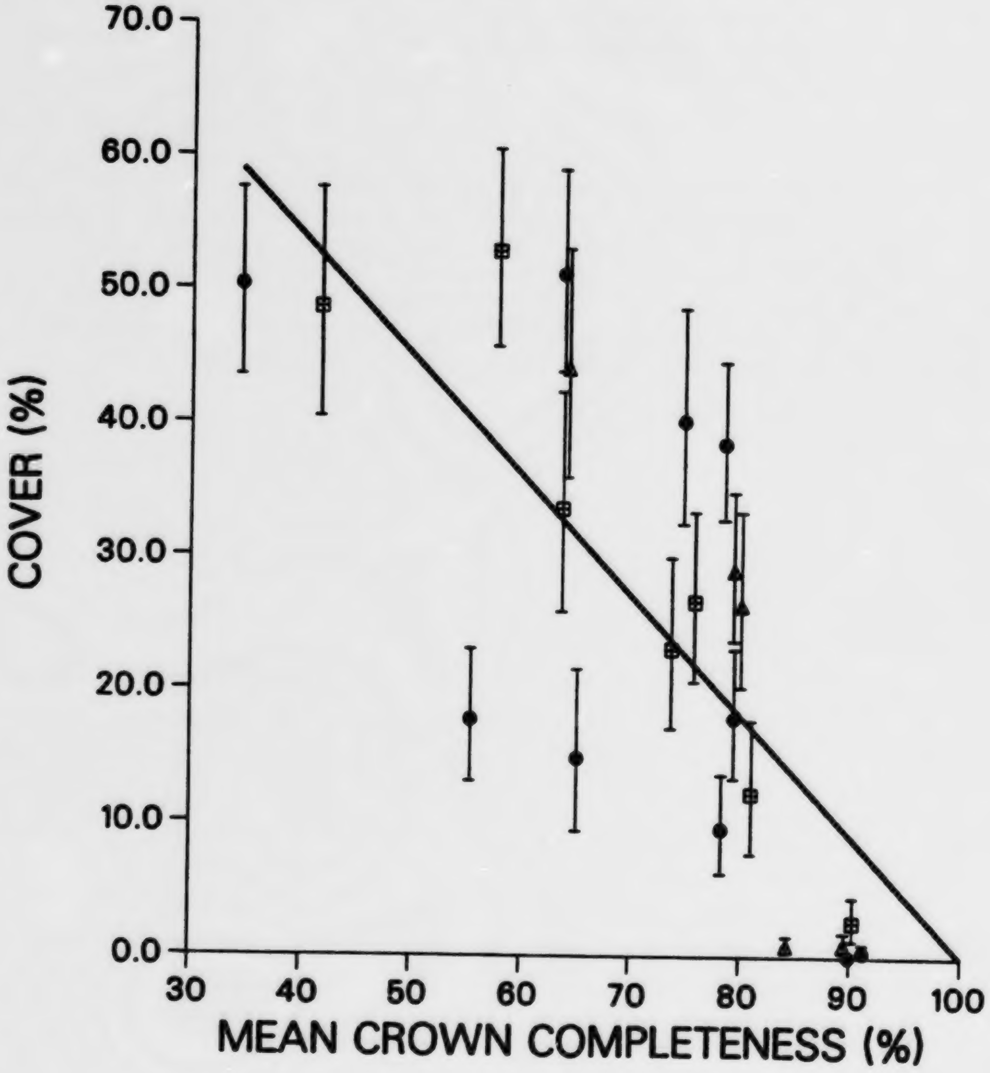

Figure 2.6. The relationship of percent cover of salal and 95% confidence intervals to mean crown completeness. CWHa (•), CWHb$_1$ (△), CWHb$_3$ (⊞). Equation represents combined data.

Because simple linear regressions already accounted for over 90% of the variation in salal density, multiple regressions either accounted for very little or no additional variation (Table 2.3). Where additional variables were significant and improved the predictability of biomass of cover equations, crown depth (CRNDEP) was the most important added variable, being included in all but one multiple regression (Table 2.3). Salal was consistently inversely related to crown depth.

Equations predicting FOLBIOM and TOTBIOM were more variable than those for CAGBIOM. The differences may be due to estimating standing crop biomass indirectly from allometric equations that were more variable than the more direct estimate of CAGBIOM.

Salal Shoot Height

Mean repose and stretch height showed considerable variability when related to MCC among the CWHa plots, but generally, shoot height peaked between 65 and 80% MCC (Fig. 2.7). $CWHb_1$ and $CWHb_3$ plots sampled within stands indicated a similar pattern of height. Shoots in some of the CWHa plots were larger than in $CWHb_3$ plots at nearly equal MCC, likely due, in part, to age differences. The relationship of salal height to other stand characteristics indicated similar patterns, though more variable than to MCC.

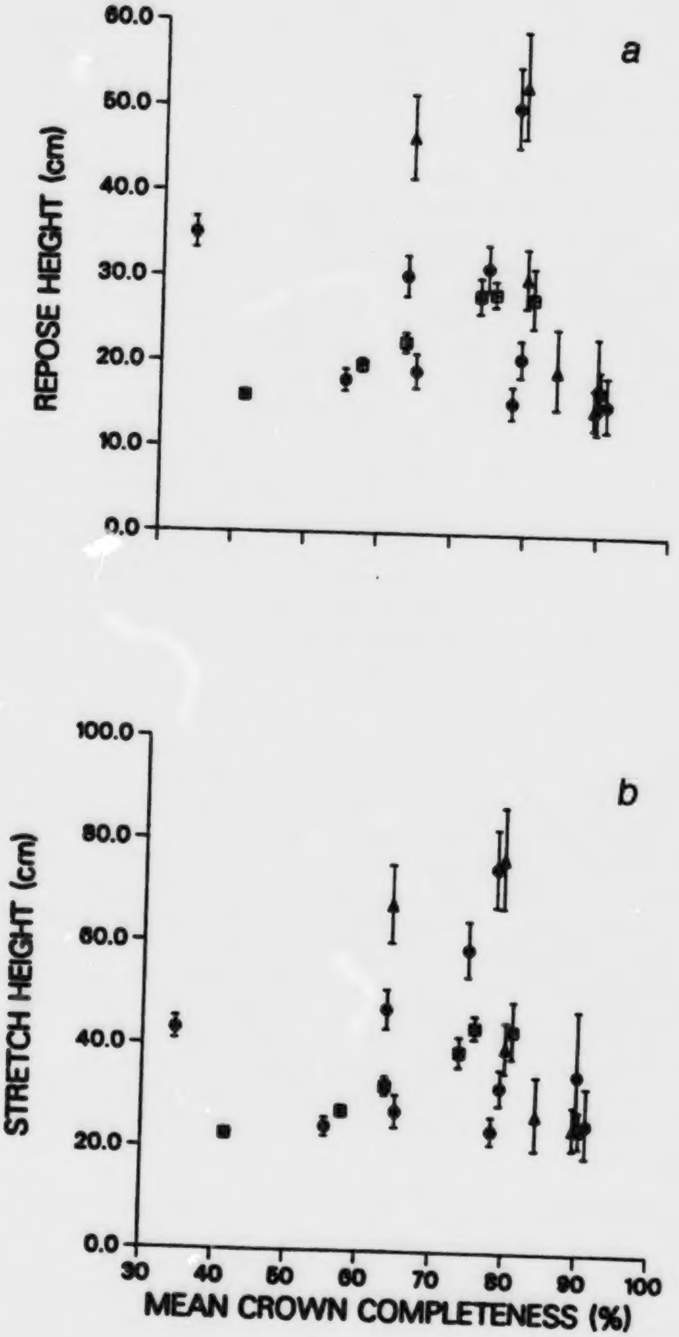

Figure 2.7. The relationship of average height of salal and 95% confidence intervals to mean crown completeness (a) repose, (b) stretch. CWHa (•), CWHb$_1$ (△), CWHb$_3$ (⊞).

DISCUSSION

Salal abundance was generally well related to forest stand characteristics in the separate variants, plant associations, and for combined data (Tables 2.2 and 2.3). Density was closely related to single stand characteristics in the two plant associations. Regressions accounted for less variation in salal biomass and cover in the CWHa than in the $CWHb_3$ variants due to age and site differences among the CWHa plots.

Differences in relationships among variants, between subzones, or between plant associations were found when testing for plant association effects on density predicted from most variables. The $CWHb_3$ plots had a greater density (Fig. 2.2) of generally smaller shoots (Fig. 2.7) than the other plots. Equations among variants did not differ for predicting current annual growth foliar biomass. Results of tests of FOLBIOM and TOTBIOM equations among variants were equivocal, and because the tests were not strictly valid, the results are somewhat inconclusive, and may be misleading (possible Type II error). Most statistical tests revealed that relationships do not differ, though there is considerable variability within variants (Figs. 2.4 and 2.5). Biomass in plots 5 and 6 was greater than other CWHa plots at a given level of an independent variable (e.g., Figs. 2.3-2.5; Appendix 24) and contributed to the greater variability of the CWHa equations. Slopes of equations among variants predicting FOLBIOM and TOTBIOM from MCC excluding plots 5 and 6 did not differ, however, the intercepts for FOLBIOM equations did differ. Plot 6 had greater productivity and biomass of salal than plot 5 even though plot 6 was in a denser forest. Plot 6, however, received more solar radiation than plot 5 (Chapters 3 and 4).

Several tests of equal regression equations were inconsistent with the majority of results. No differences were found among equations predicting density from plot BA and prism BAFSDI and BAFBA. Differences in biomass equations were found with BAFSDI, BAFBA, and several cases with NTREES and BA. All equivocal results were with a reciprocal transformation that had a more pronounced effect on ranges of overlap of independent variables than untransformed data. Prism samples accounted for patchiness of plots and pattern of variation among plots different than plot tree measurements. I conclude that the differences in relationships either among variants or between plant associations are partly a function of sampling method. Plot SDI was a measurement of plot trees rather than derived from a sample, predicted salal nearly as well as BAFSDI, and there were no differences among equations predicting salal biomass. Because plot tree measurements were more precise than prism samples and sampled the same area that salal was sampled in, I feel that tests of equal regression equations using plot measurements are the most appropriate.

Soil nutrient and moisture status and tree species were similar in both plant associations and site effects alone may not explain the differences in density. Salal shoots are very short and numerous in clearcuts and on exposed areas (plot mean density in a young clearcut as high as 189 $shoots \cdot m^{-2}$, Bunnell and Vales unpubl. data). With time, self thinning caused by competition reduces density allowing individual shoots to grow larger. As a stand develops and closes, light transmission is reduced and also there is increased competition with trees for moisture and nutrients that may affect salal. Because plots in the $CWHb_3$ were in a younger stand than most other stands sampled, the greater density may be an age effect rather than a plant association effect. No data are available on successional trends in salal density, although Long and Turner (1975), Turner and Long (1975), and Long (1977) found that salal standing crop biomass, current annual growth biomass, and cover, respectively, were greater in a 22-year-old stand than in older stands.

Other researchers have found anything from weak to strong relationships between understory and overstory in a variety of stand types (for reviews see Specht and Morgan 1981; Bartlett and Betters 1983). Forms of relationships are also diverse. Pyke and Zamora (1982) found a hyperbolic relationship of shrub production to MCC in Idaho. Bunnell and Vales (1986) found a hyperbolic relationship of salal density to MCC measured with a moosehorn and a linear one between salal cover and MCC. Bunnell and Vales (1986) stated that hyperbolic relationships would be expected for productivity variables because small changes in MCC at low levels of MCC have a greater effect on competition, throughfall, and light transmission (Chapter 3) than at higher levels of MCC. They also stated that linear relationships of understory cover to MCC would be expected because understory cover may not necessarily be related to a single productivity variable. Results of regressions here were hyperbolic for salal density and biomass and were linear for cover. The linear relationships found for some regressions in the $CWHb_3$ may be a result of a narrow range of the independent variable truncating the distribution (Bunnell and Vales 1986) or the influence of two plots. Long and Turner (1975) presented an inverse curvilinear relationship of salal biomass to foliage biomass of forest overstory.

The best independent variables (lowest $s_{y.x}$'s) predicting salal were consistent among dependent variables, for separate variants, and for combined data. Shaw and Ripley (1962), Young et al. (1967), and Pyke and Zamora (1982) believed that overstory cover was a better predictor of understory than basal area. Although relationships of salal to plot basal area or number of trees were acceptable, they were not as good as MCC or SUMDIA. Where equations were found not to differ among variants, MCC was almost as good as, or better than SUMDIA for combined data. Within variants, BAFSDI was a good independent variable, but because equations among variants differed for estimates of salal biomass predicted from BAFSDI, combined data equations were poorer than using MCC or SUMDIA. The difference between results of the two sampling methods was unexpected. Forest inventories derived from plot sampling are time-consuming. Point samples obtained from prism sampling are easier and quicker to sample. Smaller trees are sampled more intensively with plot sampling because trees are sampled with probability proportional to tree frequency, whereas point sampling is proportional to size and larger diameter trees are sampled with the same intensity as smaller diameter classes (Watts 1983). Smaller trees probably influence the understory by reducing transmission of radiation or by competition. With a large enough sample size, results of point sampling will approximate those of plot sampling (J.H.G. Smith, pers. comm., U.B.C.).

In the CWHa where inter-plot variation was greater, regressions predicting salal density using independent variables derived from samples of the stand (prism) were poorer than using plot samples. Salal biomass and cover, however, were well related to prism samples in separate variants (Table 2.2). Prism samples included trees both inside and outside the plot which would have an influence on transmission of solar radiation. Trees inside the plot would be competing for soil moisture and nutrients, and also influence transmission of radiation.

The independent variables selected in regressions suggest that solar radiation is important for salal density and biomass. Anderson et al. (1969) and Zavitkovski (1976) found positive relationships between understory abundance and solar radiation under forest canopies. Alaback (1982) believed that transmisison of solar radiation was important for understory growth, but that indirect measures of forest structure were difficult to use as causal factors affecting understory. Transmission of solar radiation has been found to be related to MCC, SUMDIS, and basal area (e.g., Wellner 1948; Miller 1959), with MCC and SUMDIA being better predictors than basal area (Chapter 3). Overstory foliage and consequently competition (Horn 1971) is also correlated with MCC and SUMBIA. Because salal density was strongly related to single plot variables, density is probably strongly influenced by inter-specific competition with trees as well as by intra-specific competition and radiation., consequently affecting biomass per unit area. Multiple regressions predicting salal biomass and cover included CRNDEP, which affects transmission of solar radiation and would be correlated with stand age and competition through tree spacing and amount of overstory foliage. The relationships between salal abundance and transmission of solar radiation are examined in Chapter 4.

Salal height has not been extensively studied. Koch (1983) found an inverse linear relationship of average shoot height to MCC between 30 and 91% MCC, and basal area 0 to 66 $m^2 \cdot ha^{-1}$ based on five plots. Bunnell and Vales (1986) found a parabolic relationship of average height to MCC measured with a moosehorn on 19 plots. The consistent peak found in this study of salal height under MCC between 65 to 80% among the three variants indicates that a parabolic relationship may apply for different sites. The location of the peak, however, may vary with age, density (competition), or microsite differences. Shoots in stands of the same age may be shorter in more open areas either because of moisture stress (Swank 1972) or no competition for light. Very dense canopies reduce incoming light, potentially limiting photosynthesis, and consequently height growth. Tall shoots under moderately dense canopies would allow forage to be more available during winter because such canopies intercept snow effectively (Bunnell et al. 1985) and tall shoots are less likely to be buried.

The results indicate that salal abundance is related to stand characteristics. It is difficult to say, however, whether salal forage would respond to thinning in agreement with predictions made from the equations in this study. Salal abundance estimates predicted from timber inventory data are possible for sites with characteristics similar to those sampled here (immature, untreated, south-southwest aspects, specific plant associations).

The method of forest sampling (e.g., plot or point samples) would determine which equations to use. I recommend using either MCC or SUMDIA because tests of equations among variants were unequivocal and these two variables had high predictabilities (Tables 2.2 and 2.3). Because relationships are curvilinear, salal foliar productivity and foliar biomass are about double at 65% MCC compared to 80% MCC for combined data equations. The optimum tradeoff between snow interception, salal productivity, and shoot height may occur around 65-70% MCC.

Salal control through stand density management is also possible. Salal abundances were at a minimum in plots 1, 9, 11, and 26 having Reineke's (1933) stand density indices (based on plot tree measurements) of 974, 1335, 1243, and 1005, respectively. Stands having SDI's greater than 1000 would probably have an adverse effect on salal, although site effects (e.g., moisture regime or steep slopes allowing considerable sidelighting) may support higher abundances of salal than expected (as in plots 4, 13-15, and 23 with plot SDI's of 1201, 1388, 1544, 1397, and 1028, respectively). These plots, however, were influenced by sidelighting because they were located in dense stand patches with a relatively open stand outside the plot (BAFSDI was considerably lower than plot SDI for all of these plots).

CONCLUSION

The functional relationship of salal density to forest overstory characteristics is different in the two plant associations studied, but the difference may be due to age effects. Simple linear regressions with overstory characteristics as independent variables accounted for 90% or more of the variation in salal density among sampled plots.

The relationships of salal productivity, biomass and cover to forest stand characteristics are not different between plant associations. For combined data and using independent variables obtained from plot samples, simple linear regressions accounted for 58-82% of variation in salal biomass and cover. Multiple regressions including crown depth improved the predictability of the equations. Relationships developed among stands of different ages and locations were more variable than relationships developed within stands.

Relationships between salal understory and forest overstory were generally hyperbolic, but some equations were linear. The best forest stand characteristics to use to predict salal abundance are mean crown completeness, sum of tree diameters, or stand density index.

Salal height was greatest between 65 and 80% MCC. Although mean shoot height was less in the $CWHb_3$ variant, the shape of the relationship was the same among the three variants sampled.

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CHAPTER 3. RELATIONSHIPS BETWEEN TRANSMISSION OF SOLAR RADIATION AND FOREST STAND CHARACTERISTICS

INTRODUCTION

Transmission of shortwave solar radiation into forest stands has been evaluated empirically (e.g., Wellner 1948; Miller 1959; Vezina and Pech 1964) and discussed or modeled theoretically (e.g., Anderson 1966; Cowan 1968; Lemeur 1973; Norman 1975; Norman and Jarvis 1975; Ross 1981; Baldocchi et al. 1985). Solar radiation under forest canopies has been related to snow melt (e.g., Miller 1959), understory growth (Anderson et al. 1969; Zavitkovski 1976; Chapter 4), deer and elk thermal cover (Bunnell et al. 1986), and production efficiency (e.g., Zavitkovski 1976). Predicting solar radiation under forest canopies can be done using stand characteristics (e.g., Miller 1959; Perry et al. 1969) or with hemispherical photography (Evans and Coombe 1959; Anderson 1964a; Madgwick and Brumfield 1969). Hemispherical photography has the advantage of being widely applicable, but is affected by exposure conditions. Relationships between transmission and stand characteristics among sites may differ because of stand structure or species composition (Wellner 1948), or methods of sampling predictor variables (Bunnell and Vales 1986). Crown closure, basal area, number of trees, and stand density (sum of diameters) have been the most common predictor variables.

Some researchers have studied transmission of separate radiation components into forest stands (e.g., Muller 1971; Reifsnyder et al. 1971/72; Hutchison and Matt 1977; Baldocchi et al. 1984a, 1984b). Anderson (1964b) stressed the importance of appropriate instrumentation, sample design, and separation of radiation components because each are intercepted differently by the canopy. Reifsnyder et al. (1971/72) and Gay et al. (1971) demonstrated the importance of considering the spatial variation of penetration of radiation.

This study examined the penetration of the global, direct, diffuse, and diffuse photosynthetically active (measured as photon flux density, PPFD, 0.4-0.7 μm) components of solar radiation (0.3-3.0 μm) into immature coniferous forest stands on Vancouver Island, British Columbia. Specific objectives were to: (1) develop regressions predicting transmission of solar radiation components from forest stand characteristics; (2) determine if the relationships were different between stands of different structures; and (3) assess the degree to which the hemispherical photograph method of Anderson (1964a) as adapted by Vales and Bunnell (1986) predicts transmission of diffuse, diffuse PPFD, and direct radiation.

STUDY AREAS

Twelve plots were sampled at several locations on Vancouver Island, British Columbia, Canada. Six plots were in the Coastal Western Hemlock dry subzone (CWHa; Krajina 1965) and 6 were in the CWH wet subzone (CWHb). The CWHa plots were separated geographically and in stands of different ages and structures. CWHb plots were all located in the same stand with less than 800 m between the farthest separated plots. The CWHb stand was younger, with smaller trees than stands in the CWHa (Table 3.1). Because the two subzones were represented by stands with broad structural differences, future references to subzones will be synonymous with structural differences.

All plots were in immature stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn). Additional species found in the CWHb stand were amabilis fir (*Abies amabilis* (Dougl.) Forbes), yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), and western white pine (*Pinus monticola* Dougl.).

Plots were selected to encompass a range of overstory cover. Criteria used to locate plots were: homogeneous canopy structure, no deciduous trees, stand age 30-60 years, no stand treatment (e.g., no thinning or fertilization), slopes 10-60%, south-southwest aspects, and elevation 200-600 m.

TABLE 3.1 Descriptions of plots used to sample solar radiation and forest stand characteristics

Plot	Latitude-Longitude	Aspect (°)	Elev. (m)	Slope (%)	Age	MCC[a]	Spp. Comp.[b] DF-WH-Misc	NTREES[c] (#/ha)	BA[c] (m^2/ha)	Avg. DBH[c] (mm)	Avg. Ht.[c] (m)	CRNDEP[c] (m)
1[d]	50°12′ - 126°28′	230	430	30	28	0.91	28-72- 0	2533	37.7	131	12.4	9.4
2[d]	50°07′ - 125°39′	215	270	15	37	0.78	61-23- 0	1600	46.7	173	13.6	10.1
5[d]	48°54′ - 124°18′	206	310	52	60	0.64	100- 0- 0	756	35.0	235	25.2	7.3
6[d]	48°54′ - 124°18′	215	310	45	59	0.78	100- 0- 0	1733	34.4	145	15.6	5.8
7[d]	48°54′ - 124°18′	173	200	9	34	0.35	8-92- 0	267	14.8	219	15.7	13.1
9[d]	48°49′ - 124°19′	261	630	43	42	0.90	37-62- 1	2711	54.9	149	15.0	7.9
21[e]	48°36′ - 123°52′	240	570	30	30	0.58	97- 3- 0	889	10.1	110	9.7	8.9
22[e]	48°36′ - 123°52′	240	570	30	30	0.42	100- 0- 0	756	8.5	118	10.3	9.8
23[e]	48°36′ - 123°52′	220	570	20	30	0.81	74-20- 6	2222	41.6	144	13.4	11.3
24[e]	48°36′ - 123°52′	220	570	20	30	0.64	64-11-25	1111	26.1	159	14.3	12.8
26[e]	48°36′ - 123°52′	219	550	19	30	0.90	28-62-10	2622	38.9	128	12.7	9.3
27[e]	48°36′ - 123°52′	214	600	22	30	0.76	52-30-18	1378	17.5	119	11.5	8.7

[a] Mean crown completeness estimate of forest overstory cover.

[b] Percent of species by basal area contribution. DF=Douglas-fir, WH=western hemlock, Misc=other coniferous species.

[c] Determined from trees ≥ 8.0 cm DBH.

[d] Plots in CWHa subzone.

[e] Plots in CWHb subzone.

METHODS

Overstory Sampling

Forest overstory cover is termed "mean crown completeness" (MCC) sensu Bunnell et al. (1985:181) and is defined to include holes within as well as between tree crowns. Plots (9 x 25 m, 0.0225 ha) were laid out along slope contours and MCC was systematically sampled at 52 points within each plot using a 10° arc moosehorn (Robinson 1947; Bonnor 1967). The sample design provided complete coverage of the canopy above each plot.

Two designs were used to sample additional stand characteristics. Tree species, diameter at breast height (DBH), top height, and height to base of live crown (HBLC; height where lowest live branches were attached to the bole) were recorded for all trees $\geq$ 8.0 cm DBH inside the plot. Trees < 8.0 cm DBH and > 20 cm tall were counted. Point samples were taken with a 4 basal area factor (BAF_4) prism at the four plot corners and at plot center. Species and DBH of "in" trees were recorded for the prism samples. Samples of trees only in the plot reflect processes acting within the plot. Prism samples included trees outside the plot and integrate processes acting within as well as from angles outside the plot. Plot overstory characteristics are summarized in Table 3.1.

Five hemispherical photographs were taken within each plot and analyzed for diffuse and direct site factors (sensu Anderson 1964a) using the method described by Vales and Bunnell (1986).

Solar Radiation Sampling

Shortwave solar radiation (0.3-3.0 μm) was monitored with paired Dome solarimeters (Lintronic Ltd.) recorded on CR-21 data loggers as 3-minute averages of samples taken at 1-minute intervals. Shadow bands (Horowitz 1969) separated diffuse from global radiation with sensors mounted 1.5 m above ground and paired on each stand. Ideally, Drummond's (1956) correction factor should be applied to sensors outside a forest and a different correction term, developed for under forest canopies, should be applied to the below-canopy sensors. Because appropriate corrections for below-canopy sensors have not been explored, and the same correction term applied to both open and canopy sensors would not affect relative amounts of radiation, no corrections were made to diffuse sensors. Hutchison and Matt (1977) argued that no correction term should be applied to diffuse sensors because below-canopy diffuse radiation results from multiple reflections and transmission through leaves, and that the distribution of brightness under a canopy is different from that above.

One pair of sensors recorded solar radiation in an open area near the plot to determine the amount of radiation potentially above the canopy. Two pairs of sensors were located 11 m apart within plots, along the centerline, and 7 m in from each edge. One LI-COR LI-190SB quantum sensor was shaded and monitored diffuse photosynthetic photon flux density radiation (PPFD; 0.4-0.7 μm) in the plot center as 3-minute averages of 1-minute samples.

The Dome solarimeters were calibrated against a reference Kipp & Zonen solarimeter. Calibrations were curvilinear over the entire range (Matt and

Hutchison 1974 cited in Hutchison and Matt 1977). A linear calibration based on data less than 150 $W \cdot m^{-2}$ was applied to all diffuse sensors because diffuse radiation rarely exceeded 150 $W \cdot m^{-2}$. Had the full-range calibration been applied, the amount of diffuse radiation would have been overestimated. The open diffuse solarimeter was calibrated against the quantum sensor to obtain an equation predicting diffuse PPFD above the canopy. The results of the calibration indicated that 65% of diffuse shortwave irradiance was in the 0.4-0.7 μm waveband on an energy flux basis (using 4.24 μE/J of McCree 1972 and McCartney 1978 to convert to J in the photosynthetically active radiation waveband), or there was 2.756 μE of photosynthetically active radiation photons per J of diffuse shortwave solar radiation. These values are in agreement with Ross (1975), but are lower than those of Szeicz (1974).

Below-canopy diffuse radiation is composed of diffuse radiation from the sky transmitted through the canopy, reflected diffuse, and scattered direct beam radiation (Reifsnyder et al. 1971/72). The proportion of diffuse radiation transmitted that was measured included all three components and is not the true fraction of above-canopy diffuse sky radiation that was transmitted.

Direct radiation was obtained by subtracting the diffuse radiation component from global radiation. Transmission of each component was computed by dividing the average daily sum of the two below-canopy sensors by the daily sum of open radiation. Differences between diffuse sensors under the canopy were consistent among plots indicating little spatial variation of diffuse radiation under canopies. Differences between global sensors were variable among plots and demonstrated the spatial variation due to sunflecks. Only days that were clear or mostly sunny were used for analyses (ratio open diffuse/open global < 0.20). Each plot was monitored for at least one full day. Because variable weather conditions did not always permit monitoring a plot during one full clear day, half-day (sunrise to solar noon) monitoring was multiplied by 2 for two cases. Transmission was averaged for plots sampled over two days.

Definition of Variables

GLOBAL - proportion of global solar radiation transmitted
DIRECT - proportion of direct solar radiation transmitted
DIFFUSE - proportion of diffuse solar radiation transmitted (included downward scattering of direct beam in tree canopies)
PAR - photosynthetically active radiation as a proportion of diffuse PPFD transmitted
MCC - mean crown completeness (average of 52 moosehorn samples and reported as a fraction)
SUMDIA - sum of DBH (mm/225 m^2) of plot trees > 8.0 cm
BA - basal area ($m^2 \cdot ha^{-1}$) of plot trees > 8.0 cm
DBH_q - diameter of tree of average basal area (quadratic mean diameter)
NTREES - number of plot trees$\cdot ha^{-1}$ > 8.0 cm
SDI - Reineke's "stand density index" (Reineke 1933) computed from: $SDI = NTREES \cdot (DBH_q/25)^{1.6}$ (Long 1985)
BAFBA - average stand basal area ($m^2 \cdot ha^{-1}$) of trees >8.0 cm determined from 5 BAF_4 prism samples
BAFTREES- average number of trees$\cdot ha^{-1}$ > 8.0 cm determined from 5 BAF_4 prism samples

BAFSDI - Reineke's SDI determined from prism sampling computed from $\mathrm{BAFTREES} \cdot (\mathrm{BAFDBH}_q/25)^{1.6}$

Analyses

The proportion transmitted of each radiation component was regressed against stand characteristics using simple linear, second-degree polynomial, and nonlinear (e^{-bX}, ae^{-bX}) regressions. Independent variables were either untransformed, natural log, or reciprocally transformed. The best regressions were identified as having the lowest standard error of the estimate ($s_{y.x}$), with a high r^2 (i^2 in the nonlinear regressions, Ezekiel and Fox 1970), and no trend in the residuals. For a given dependent variable, the best form of regression for one independent variable was not necessarily the best form for a different independent variable. Radiation components also differed in the best forms of regressions with direct and global radiation regressions being different from diffuse regressions.

Generally the nonlinear ae^{-bX} form was ranked the best form of regression for all radiation components across all independent variables in the separate subzones. This form does not depart greatly from Beer's law presented by Monsi and Saeki (1953), e^{-kz}, with stand characteristics being correlates of z, cumulative leaf area index (LAI). I also used the e^{-bX} form to explore how radiation components may be intercepted by stand characteristics. The ae^{-bX} form would give an unrealistic estimate in open areas with an a coefficient other than 1.0.

Tests of equal regression slopes and equations between subzones were computed with covariance analysis using the UBC SLTEST program (Le 1971). Tests were made on linear forms using log and reciprocally transformed independent variables because these forms of regressions usually had only modestly larger $s_{y.x}$'s than the ae^{-bX} form, and because tests were not available for the nonlinear form.

Regressions developed in individual subzones are presented for all radiation components and for combined data of GLOBAL, DIRECT, and PAR. This manner of presentation illustrates the relationship among stands (CWHa) compared to within a stand (CWHb) and the strength of the relationship when all are combined. Paired t-tests within subzones and across all plots were used to test the diffuse and direct site factors estimated from hemispherical photographs against measured DIFFUSE, PAR, and DIRECT.

Data manipulation and some analyses were done using MIDAS (Fox and Guire 1976). A FORTRAN program with a derivative-free, parameter-estimating nonlinear regression subroutine (Moore 1984) computed nonlinear regressions, $s_{y.x}$'s, and i^2's.

RESULTS AND DISCUSSION

Proportions Transmitted

Daily radiation loads in the open and below the canopy are summarized (Table 3.2). Open global shortwave radiation ranged from 22 to 29 $MJ \cdot m^{-2} \cdot d^{-1}$ and open diffuse was 7 to 15% of the total. Below-canopy fluxes depended upon openness of the plot. Diffuse radiation below the canopy ranged from 18 to 91% (plots 7 and 23, respectively) of global. Hardy (1975) found below-canopy diffuse to be 36% of the total in a 10-m tall 21 year-old Douglas-fir stand. Gay et al. (1971) reported an increase of the diffuse/global ratio from 15% above to 46% below a *Pinus taeda* L. canopy. The increase in proportion of below-canopy diffuse is due to reflection and scattering of direct beam radiation (Hutchison and Matt 1976). The amount of diffuse photosynthetically active radiant energy in below-canopy diffuse shortwave radiation was estimated roughly at 2-24% by assuming 4.24 μE/J for conversion, or was 0.1-1.02 μE/J PPFD to diffuse shortwave solar irradiance (Table 3.2). Baldocchi et al. (1984a) found ratios of below-canopy global photosynthetically active radiant energy to global shortwave between 22 and 29% in a hardwood forest. Absorption of PPFD by the canopy was evident by the decreased proportion of diffuse PPFD in diffuse shortwave radiation below the canopy compared to the open (Table 3.2).

Variability in the ratio of diffuse PPFD to diffuse shortwave energy flux was associated with stand structure. There were significant ($p < 0.05$, $n = 12$) negative correlations between the below-canopy ratio of PPFD/diffuse and stand characteristics (MCC, SUMDIA, BA, NTREES). Baldocchi et al. (1986) found variation in the below-canopy ratio of global photosynthetically active radiant energy/global shortwave energy with changes in solar altitude within a single stand.

Ranges of proportions of radiation transmitted by the forest canopy were 0.03 to 0.57 for GLOBAL (plots 1 and 22, respectively), 0.005 to 0.43 for DIRECT (plots 26 and 7), and 0.01 to 0.29 for PAR (plots 1 and 7). The proportion of diffuse shortwave radiation transmitted differed dramatically between the two stand structures. The proportion of diffuse radiation transmitted by CWHa plots was 0.18 to 0.78, but the proportion transmitted by CWHb plots was 0.34 to 1.80. The bases of tree crowns in the CWHa were higher than in the CWHb stand and HBLC was above the sensors in the CWHa. Sensors were located within tree crowns in the CWHb plots (crowns extended nearly to the ground) and recorded reflected direct beam radiation occurring within tree crowns. Miller (1967, 1969) reported higher estimates of diffuse and global solar radiation in the upper portions of *Populus tremuloides* Michx. and *Quercus gambelii* Nutt. canopies than above the canopy. Muller (1971) also reported several cases where below-canopy global irradiance exceeded the irradiance in the open. Hardy (1975) found that 73% and 31% of diffuse solar radiation was transmitted to the 5 m and ground levels in a 10 m tall unthinned Douglas-fir stand.

Figure 3.1 illustrates a time plot of open and canopy global and diffuse radiation for plot 27 (proportion of diffuse transmitted 1.29). Canopy diffuse and global are much less than open global and sunflecks are evident as peaks in the below-canopy global curve. The below-canopy diffuse curve rises above the open diffuse curve.

TABLE 3.2 Daily sums of solar radiation components by plot

Plot	Date	Noon solar altitude (°)	Open radiation					Canopy radiation				
			Global (MJ·m^{-2}·day^{-1})	Diffuse (MJ·m^{-2}·day^{-1})	Direct (MJ·m^{-2}·day^{-1})	PPFD[a] ($Em^{-2}d^{-1}$)	Dif/G[b]	Global[c] (MJ·m^{-2}·day^{-1})	Diffuse[c] (MJ·m^{-2}·day^{-1})	Direct (MJ·m^{-2}·day^{-1})	PPFD[a] ($Em^{-2}d^{-1}$)	PPFD/Dif[d]
1[e]	22-23/7/84	60	28.97	3.08	25.89	8.50	0.106	0.763	0.546	0.217	0.084	0.153
2	1/8/84	58	25.97	1.79	24.19	4.92	0.069	1.931	0.644	1.288	0.244	0.379
5[f]	19-20/8/84	54	22.44	3.27	19.18	9.00	0.146	1.642	0.750	0.892	0.632	0.810
6	22/8/84	53	23.00	3.31	19.69	9.12	0.144	2.082	0.946	1.136	0.799	0.845
7[g]	1/9/84	50	21.99	2.31	19.68	6.37	0.105	10.230	1.793	8.437	1.823	1.017
9[e]	3-4/7/85	64	27.48	2.51	24.97	6.92	0.091	1.112	0.776	0.336	0.079	0.102
21	13/7/85	63	27.82	3.19	24.63	8.80	0.115	7.701	4.562	3.139	2.295	0.503
22	17/7/85	63	26.97	2.94	24.03	8.09	0.109	15.279	5.283	9.995	1.750	0.331
23[e]	19-20/7/85	62	27.50	2.57	24.93	7.08	0.094	1.598	1.462	0.136	0.257	0.176
24	26/7/85	61	26.91	2.42	24.49	6.66	0.090	3.644	2.785	0.859	0.747	0.268
26	15/8/85	56	26.13	2.34	23.79	6.44	0.089	0.908	0.791	0.117	0.106	0.134
27	17/8/85	55	25.48	2.09	23.39	5.76	0.082	3.614	2.704	0.911	0.462	0.171

[a] Diffuse photosynthetic photon flux density.

[b] Ratio open diffuse/global as an index of clear sky, < 0.20 considered as sunny.

[c] Average of two sensors.

[d] Below-canopy ratio of photosynthetic photon flux density to below-canopy diffuse solar irradiance ($\mu E \cdot J^{-1}$).

[e] Average of monitoring two days.

[f] Computed from monitoring one full day and one half-day × 2.

[g] Computed from monitoring one half-day × 2.

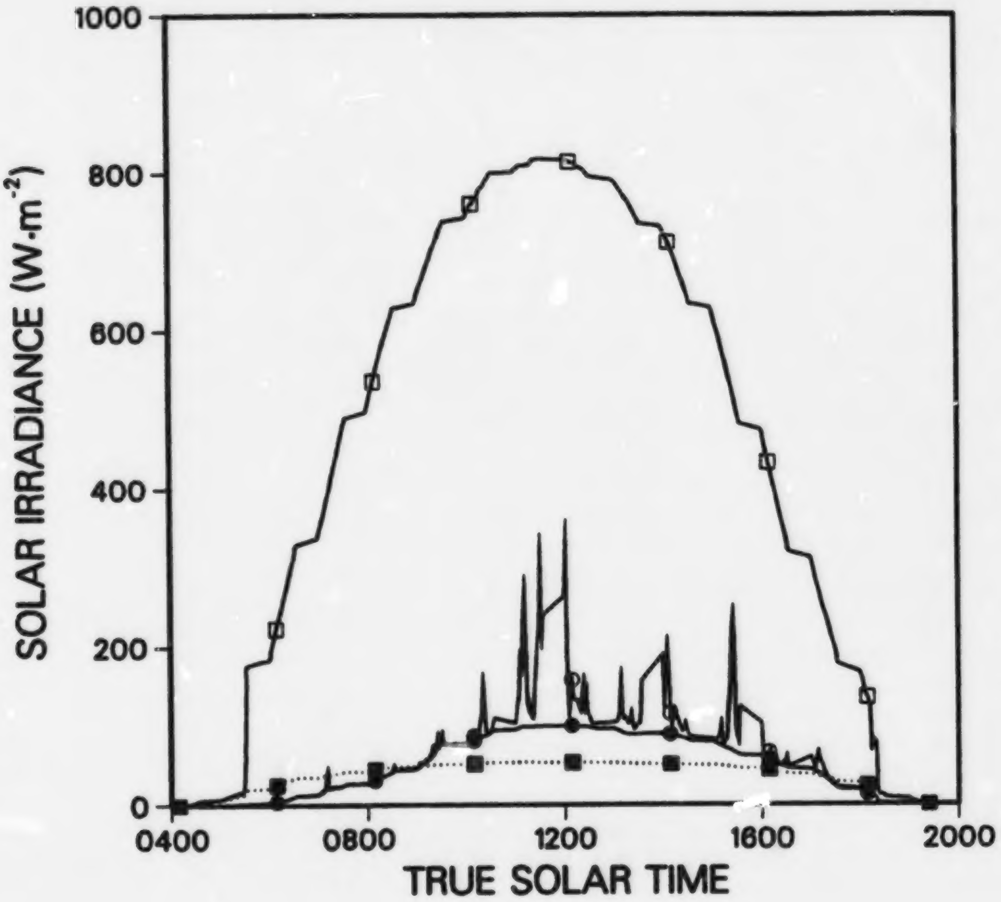

Figure 3.1. Solar irradiance as a function of time for plot 27. Open global (□) and diffuse (···■···), canopy global (o) and diffuse (•).

TABLE 3.3 Regression coefficients of equations predicting solar radiation components from forest stand characteristics. Sample sizes: CWHa=6, CWHb=6. Equations significant at $p \leq 0.05$. Regression equation: $Y = ae^{-bX}$

Y	Subzone	X	a	b	r^2	$s_{y \cdot x}$
GLOBAL:	CWHa	MCC	2.4109	4.7957	0.98	0.0282
		SUMDIA	0.8657	4.8273E-4[a]	0.96	0.0383
		SDI	1.2643	3.4154E-3	0.97	0.0324
		BAFSDI	6.8557	6.2906E-3	0.96	0.0364
	CWHb	MCC	4.8879	5.1702	0.97	0.0366
		SUMDIA	1.9707	7.2250E-4	0.85	0.0867
		SDI	1.4843	4.8465E-3	0.86	0.0830
		BAFSDI	1.5890	4.5990E-3	0.96	0.0449
	Both	MCC	2.3547	4.1668	0.86	0.0701
		SUMDIA	0.9792	4.7260E-4	0.85	0.0725
		SDI	1.1656	3.7187E-3	0.88	0.0654
		BAFSDI	1.3514	3.7443E-3	0.84	0.0761
DIFFUSE:	CWHa	MCC	1.5923	2.1929	0.85	0.0917
		SUMDIA	0.9120	1.8875E-4	0.72	0.1255
		SDI	1.1061	1.4430E-3	0.70	0.1292
		BAFSDI	N.S.[b]		0.46	0.1732
	CWHb	MCC	4.8886	2.2770	0.78	0.2848
		SUMDIA	2.6581	2.2341E-4	0.94	0.1519
		SDI	2.4254	1.4755E-3	0.92	0.1763
		BAFSDI	2.8328	1.8436E-3	0.84	0.2435
DIRECT:	CWHa	MCC	3.3782	6.0002	0.98	0.0226
		SUMDIA	0.9725	6.2694E-4	0.98	0.0283
		SDI	1.5134	4.2891E-3	0.98	0.0245
		BAFSDI	12.0179	7.7863E-3	0.98	0.0256
	CWHb	MCC	14.2767	8.4899	0.99	0.0202
		SUMDIA	1.0	6.6399E-4	0.70	0.0970
		SDI	1.0	5.3104E-3	0.77	0.0851
		BAFSDI	1.0	4.8240E-3	0.86	0.0659
	Both	MCC	3.6343	5.8766	0.93	0.0432
		SUMDIA	1.2592	7.7261E-4	0.85	0.0623
		SDI	1.5885	6.0770E-3	0.74	0.0812
		BAFSDI	1.1168	4.3206E-3	0.63	0.0972
PAR:	CWHa	MCC	1.1995	4.1655	0.95	0.0253
		SUMDIA	0.4763	3.9642E-4	0.95	0.0251
		SDI	0.6697	2.8915E-3	0.96	0.0237
		BAFSDI	2.6211	5.1752E-3	0.95	0.0253
	CWHb	MCC	0.9428	3.1579	0.67	0.0635
		SUMDIA	0.6171	4.6447E-4	0.92	0.0302
		SDI	0.4694	2.8252E-3	0.88	0.0384
		BAFSDI	0.5200	2.9551E-3	0.84	0.0447
	Both	MCC	0.9927	3.4685	0.79	0.0473
		SUMDIA	0.5100	4.0491E-4	0.93	0.0264
		SDI	0.4930	2.6627E-3	0.87	0.0367
		BAFSDI	0.5551	2.8154E-3	0.74	0.0522

[a] Exponent for power of 10.

[b] Equation not significant ($p > 0.05$).

Radiation-Forest Stand Relationships

Results of the regressions of radiation on stand characteristics found MCC, plot SUMDIA and SDI, and BAFSDI obtained from prism sampling to be the best variables predicting transmission of solar radiation (Table 3.3). Number of trees and basal area derived from plot tree measurements also were acceptable predictors. Basal area derived from prism samples was poorer than using plot BA and the regressions developed on number of trees determined by prism samples were not significant. Regressions that included number of saplings (trees < 8.0 cm DBH and > 20 cm tall) with larger trees were worse than those using larger trees alone. Stand variables representing the midstory (number of saplings), tree diameter, species composition, height, and crown depth were poor single predictors of transmission. Other studies have not reported relationships with SDI as an independent variable. SDI integrates tree size, basal area, and number of trees and should be a useful integrator of tree foliage and stand density.

Some of the equations (e.g., DIRECT versus SUMDIA, SDI in the CWHb) gave peculiar results when extrapolated outside the range of the data using the ae^{-bX} and are presented in Table 3.3 with an intercept of 1.0. The equations presented are applicable only within the range of the stand data used to develop them.

The negative exponential relationships (equations from Table 3.3) are illustrated in Fig. 3.2 as a function of MCC. Solid lines for DIFFUSE represent equations developed in individual subzones. Dotted curves in Fig. 3.2 for GLOBAL, DIRECT and PAR represent the relationships developed in individual subzones and the solid line is for combined data. The dashed line in the global graph is reproduced from Miller (1959) and is a general relationship derived from the results of several studies in *Pinus* spp. stands in which various methods were used to estimate crown closure. Vezina and Pech (1964) presented a relationship predicting transmission from crown closure estimated with a moosehorn in *Pinus banksiana* Lamb. stands that was also higher than that of Miller (1959). Differences in the curves may be related to different methods used to sample radiation (Anderson 1964b), stand structure or species composition (Wellner 1948), or differences in methods used to estimate forest overstory cover (Bunnell and Vales 1986).

Indices of determination (i^2, analagous to r^2) were computed for seven independent variables predicting radiation components using the regression form e^{-bX} (Table 3.4). This form has a regression intercept of 1 and comparison of Tables 3.3 and 3.4 indicates the importance of the equation intercepts in Table 3.3. The e^{-bX} form would be more applicable outside the range of the data and give a realistic estimate of the proportion transmitted when there is no canopy. Stand characteristics with high i^2 closely approximated the theoretical Beer's law relationship and integrated factors that served as correlates of LAI.

Where there was extensive inter-plot variation and tall HBLC's (CWHa), MCC accounted for more of the variation in transmission of diffuse radiation than plot or prism variables (Tables 3.3 and 3.4). In the CWHb, however, MCC was poorer than plot variables at predicting DIFFUSE and PAR. Determining MCC in the CWHb was difficult with measurements often being made within tree crowns rather than below them, and therefore not representing overstory cover as in the CWHa. MCC measurements also were made at the height of, or slightly above the height of radiation sensors. Extensive scatter of the direct beam

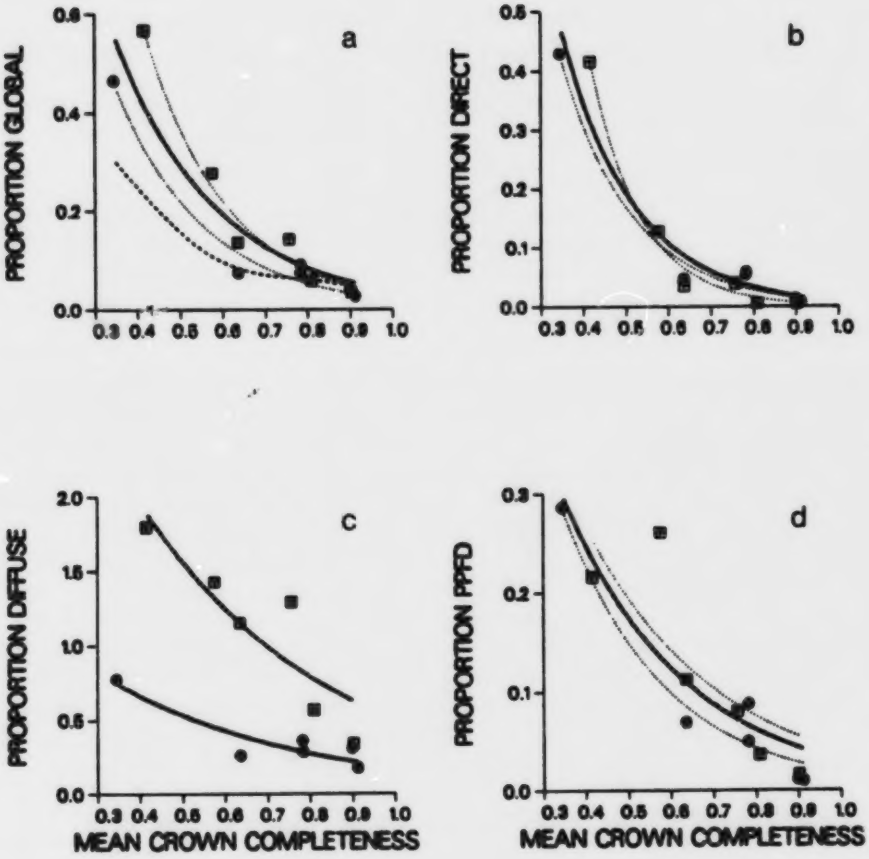

Figure 3.2. Relationships between the proportions of solar radiation components transmitted and mean crown completeness. Dotted lines in a, b, and d are relationships for individual subzones. Dashed line in a is from Miller (1959). CWHa (•), CWHb (⊞).

TABLE 3.4 Indices of determination (i^2) from regressions predicting radiation components from forest stand characteristics using the regression form $Y = e^{-bX}$

X	Global	Direct	Diffuse	PAR	Avg. rank[a]
CWHa:					
MCC	0.854	0.836	0.736	0.945	3.0
SUMDIA	0.951	0.975	0.707	0.791	2.8
NTREES	0.892	0.946	0.414	0.779	5.0
BA	0.913	0.906	0.647	0.941	3.3
SDI	0.955	0.954	0.694	0.910	2.3
BAFBA	0.706	0.698	0.427	0.821	5.5
BAFSDI	0.696	0.685	0.393	0.863	6.3
CWHb:					
MCC	0.689	0.663	0.010	0.666	6.0[b]
SUMDIA	0.802	0.702	0.021	0.882	3.7
NTREES	0.751	0.659	0.007	0.876	5.0
BA	0.834	0.779	0.034	0.678	3.7
SDI	0.842	0.771	0.030	0.738	3.3
BAFBA	0.909	0.865	0.010	0.599	3.3
BAFSDI	0.910	0.863	0.010	0.653	3.0
Combined:					
MCC	0.729	0.751	0.142	0.787	4.0[b]
SUMDIA	0.850	0.841	0.300	0.766	2.3
NTREES	0.534	0.646	0.221	0.086	6.0
BA	0.789	0.569	0.369	0.504	4.0
SDI	0.874	0.733	0.345	0.742	2.3
BAFBA	0.770	0.547	0.312	0.416	5.3
BAFSDI	0.809	0.631	0.280	0.600	4.3

[a] Average rank of $s_{y\cdot x}$ across components: 1=lowest, 6=highest.

[b] Excludes diffuse radiation rank.

within crowns of trees in the CWHb plots was poorly accounted for by MCC because stand structure affected MCC measurements.

There were slight differences between plot and prism variables. DIFFUSE was better related to the plot samples SDI and BA than to prism samples SDI and BA (Tables 3.3 and 3.4). Much of the diffuse radiation was scattered direct beam which would be reflected downward by tree crowns. Diffuse radiation in the plot would therefore be more related to overhead canopy on sunny days in summer than to trees outside the plot.

GLOBAL and DIRECT were better related to plot tree measurements in the CWHa and for combined data than to prism samples (Table 3.3 and 3.4). In the CWHb, however, GLOBAL and DIRECT were better related to prism samples. Because trees in the CWHb stand were of relatively the same size and spacing, prism sampling characterized the stand accurately. Where there was extensive inter-plot variation in tree size and spacing, however, plot samples were more representative of the stand near the sensors.

Miller (1959) believed that SUMDIA was superior to crown closure and BA as a measure of transmission. Because leaf area can be predicted from tree diameters (e.g., Gholz et al. 1976; Spittlehouse 1981), SUMDIA would integrate tree LAI and tree density. Jackson and Harper (1955), Perry et al. (1969), and my results (Table 3.4) indicated that basal area is a useful predictor of transmission, although not as good as SUMDIA or SDI.

Miller (1959) also believed that crown closure alone was not an adequate predictor of transmission because attenuation of radiation was also a function of crown depth. MCC alone did not predict transmission of direct and global radiation as well as other stand characteristics (Table 3.4). Crown depth is related to tree size and density. Stand characteristics that integrate tree size and density such as SUMDIA or SDI also integrate crown depth.

Studies have demonstrated the vertical distribution of radiation within coniferous stands (e.g., Norman and Jarvis 1974; Hardy 1975; Sinclair and Knoerr 1982) but the influence of crown depth among stands has received little attention. As a single variable crown depth did not predict transmission well, probably because of the confounding effects of stand density or MCC. Coefficients for crown depth in multiple regressions were not significantly different from zero. Any estimate of overstory cover made using an instrument with a moderately wide angle will include some depth of crowns (Pyke and Zamora 1982; Vales and Bunnell 1986; Bunnell and Vales 1986) and possibly serve as a better integrator of the three-dimensional nature of the intercepting surface. The 10° arc moosehorn, however, adequately sampled the overstory and was an acceptable variable predicting transmission. The moosehorn also shows little bias and is an accurate predictor of understory abundance (Bunnell and Vales 1986) which would be influenced by radiation (Chapter 4).

Coefficient b in the e^{-bX} equations showed a consistent pattern among overstory variables for rate of extinction of the different radiation components. Slopes were steepest (rate of extinction fastest) for transmission of PPFD, followed by direct, global, and then diffuse radiation. Canopies absorbed diffuse PPFD (Table 3.2). The drop in direct radiation transmitted was greater than global because global also contains diffuse radiation which was attenuated the slowest. Direct radiation was also converted to diffuse radiation which caused the steep slope for attenuation of direct radiation and shallow slope for enriched diffuse radiation.

Equation Differences

Linear regression equations predicting DIRECT from log and reciprocally transformed independent variables did not differ significantly between subzones (stand structures; $p > 0.05$). All regressions predicting DIFFUSE differed between subzones ($p < 0.05$). Tests of regressions predicting PAR and GLOBAL between subzones were equivocal, sometimes differing with independent variable or form of regression. The tests of equations were between broad classes of stand structure and not tests of subzone effects.

Site Factors

Paired comparisons of the diffuse site factor (estimated photographically; Anderson 1964a; Vales and Bunnell 1986) with measured transmission (Table 3.5) within subzones and including all plots found differences between the diffuse site factor and the proportions transmitted of diffuse radiation and PAR ($p < 0.05$, $n = 11$). The diffuse site factor was lower than the measured transmission of diffuse and higher than PAR (Table 3.5). No difference was found between the direct site factor and measured transmission of direct radiation over all plots ($p > 0.05$, $n = 11$), although the direct site factor was much higher on all but 2 plots. Tests excluding plots 7 and 22 found significant differences ($p < 0.05$, $n = 9$). Plots 7 and 22 were the most open plots and were more spatially heterogeneous than denser plots.

Lower measured transmission of direct radiation may be a result of sensor locations being different from photograph points and the spatial variability of direction radiation. The direct site factor was for 21 March to 23 September rather than just for the days sampled for radiation. An analysis was also done using the direct site factor obtained from the solar path only for days when radiation was sampled. This site factor was higher (more open) than for the entire summer. Hourly comparisons between the direct site factor for days when radiation was sampled and hourly measured proportions transmitted were significantly different ($p < 0.05$). The direct site factor used was for eight hours centered on solar noon. Comparisons between the direct site factor and measured proportions transmitted calculated for the same 8-hour period were also significantly different ($p < 0.05$). The proportion of direct radiation transmitted may have been low because of scattering of the direct beam and converting it to diffuse radiation. Small gaps in the canopy that were seen on the photos were assumed to transmit the full intensity of direct radiation. But many of these gaps were smaller than the sun's diameter (0.5°), consequently diffusing the direct beam, and reducing the proportion transmitted. A more accurate assessment of the direct site factor may be made if consideration is given to the relationship among tree height, sun diameter, and distance and angle of a canopy gap (e.g., Muller 1971:3) from the photograph location.

Anderson (1964a) and Lindroth and Perttu (1981) found agreement between estimated and measured canopy transmission. Bunnell and Vales (1986) found that the relationship between salal (*Gaultheria shallon* Pursh) understory

TABLE 3.5 Comparison of diffuse and direct site factors obtained from hemispherical photographs to measured proportions of solar radiation components transmitted

Plot	Diffuse[a] site factor	Diffuse[b]	Diffuse[b] PAR	Direct[a] site factor	Direct[b]
1	0.092	0.177	0.010	0.139	0.008
2	0.119	0.360	0.050	0.180	0.053
5	0.126	0.260	0.069	0.153	0.046
6	0.111	0.286	0.088	0.193	0.058
7	0.318	0.775	0.286	0.258	0.429
21	0.239	1.429	0.261	0.170	0.127
22	0.248	1.799	0.216	0.185	0.416
23	0.112	0.569	0.036	0.089	0.006
24	0.150	1.153	0.112	0.114	0.035
26	0.072	0.338	0.016	0.151	0.005
27	0.108	1.293	0.080	0.140	0.039

[a] Estimated from hemispherical photographs.

[b] Measured proportion of solar radiation transmitted.

abundance and site factors was poorer than relationships developed from other methods used to estimate overstory cover. Additional data (Chapter 4 and Appendix 21) indicated that salal abundance was more closely related to measured transmission of solar radiation than to either diffuse or direct site factors. The understory, however, may be regulated by transmission of radiation during a short time of the year other than the time of year sampled by the site factors I used.

Anderson's (1964a) diffuse site factor is an average over a year and is for diffuse sky radiation assuming a standard overcast sky brightness distribution. Differences found here may arise from plots being sampled for only a short time period, because of diffuse enrichment by direct beam scattering, or because of sampling radiation on sunny days with a different sky brightness distribution. Because much of the below-canopy diffuse radiation originated from the scatter of direct beam radiation, the measured proportion of diffuse radiation transmitted was higher than the diffuse site factor for diffuse sky radiation. Anderson (1964a) stated that photographic estimation of the diffuse site factor can be in error for one particular day. Lower diffuse site factors may also be attributed to photographs being deliberately underexposed to obtain contrast, but this does not explain the overestimate of the direct site factor.

Generality of Equations

A discussion on the generality of equations presented in this study requires understanding of how proportions of the different radiation components transmitted are affected by cloudiness and solar altitude within and among stands. Diffuse and direct radiation are transmitted differently, are each affected by stand structure, and interact to affect the proportion of global radiation transmitted. I will briefly discuss how transmission of diffuse, direct, and global radiation are affected by clouds and solar altitude within a stand, and apply the discussion to differences in stand structure among stands.

Anderson (1970) concluded and Reifsnyder et al. (1971/72) assumed that the fraction of diffuse sky radiation transmitted by a forest is not much affected by weather. Relationships developed here are based on transmission of diffuse radiation that included below-canopy direct beam scattering. With increasing cloudiness, the amount of direct radiation in above-canopy global radiation is reduced and there is less direct radiation available for scattering in canopies. Proportions of diffuse radiation transmitted that include direct-beam scattering should decrease with increasing cloudiness. The proportions of diffuse radiation transmitted by canopies decreased with increased cloud cover on 8 of 8 plots that were sampled over 2 full consecutive days with 2 different cloud conditions. Proportions transmitted by the CWHb plots were less than 1.0 with increasing clouds. Hutchison and Matt (1977) found a decrease in the proportion of diffuse radiation transmitted on overcast days compared to clear days in a hardwood stand, demonstrating the influence of scattered direct beam radiation (Hutchison and Matt 1976). Muller (1971) reported that downward scatter of direct radiation was about one-half of the total diffuse radiation below *Pinus* spp. canopies, and that scattering was greatest in open stands. He concluded that under clear-sky conditions, the primary source of diffuse radiation below canopies was from scattering of direct radiation by tree crowns. Scattered direct was about one-third of the total diffuse radiation below a *Pinus resinosa* Ait. canopy in Reifsnyder et al.'s (1971/72) study. If the estimated diffuse site factor accurately reflects the proportion of diffuse sky radiation transmitted, then scattering of direct beam accounted for 50 to 92% of the diffuse radiation below canopies in this study. Because much of the diffuse sky radiation penetration comes from 10° of the solar disk on clear days, transmission of diffuse is dependent on canopy openings near the path of the sun (Hutchison et al. 1980). Changing solar altitude will affect direct beam scattering (Hutchison and Matt 1976) and canopy openings in the solar path generally increase with angle above the horizon (Hutchison et al. 1980; Lindroth and Perttu 1981). There is less scattering of direct beam in tree canopies as cloudiness increases, and the equations presented will not accurately predict transmission of diffuse radiation on cloudy days and at other times of the year.

Little information is available on the effects of clouds on the proportion of direct radiation transmission. I found that the proportion of direct radiation transmitted increased with increasing cloudiness on five of eight plots. The increased transmission was unexpected and may be due to errors in the way direct radiation was calculated (global-diffuse) and lack of correction factor for the shaded sensor. The three plots in which transmission of direct decreased were the most open and had the highest direct site factors. For clear days, decreasing solar altitude would decrease the proportion of direct radiation transmitted (Anderson 1970) provided gap frequency decreased from zenith to horizon. If relative gap frequency in the solar angles, then a change in solar altitude may affect all plots similarly under clear skies. The slope of the predictive equations would remain the same, but the intercept would change. Adding a term to account for solar altitude (β) to the regression equations (e.g., $ae^{bX(\csc\beta-1)}$ Jarvis et al. 1976) may improve the accuracy of predictions under clear sky conditions at another time of the year. The effects of increasing clouds, however, would complicate the relationship of transmission of direct radiation to stand characteristics over a range of solar altitudes.

Miller (1959) cited several studies where the proportion of global radiation transmitted increased with increasing cloudiness. Zavitkovski (1974) and Hutchison and Matt (1977) found opposite results. I found that in 5 of 8 plots the proportion of global radiation transmitted increased with increasing cloud cover, though irradiance was lower than on sunny days. Stand structure would affect the proportion of global transmitted. If there are gaps in the path of the sun transmitting appreciable direct radiation on sunny days, and on cloudy days light is transmitted through gaps at all angles, then the proportion of global radiation transmitted may decrease on cloudy days in a plot with a dense overhead canopy. On the other hand, if a plot transmits little direct radiation, but has gaps in areas of the canopy other than in the solar path, then the proportion of global radiation transmitted may increase on cloudy days. Those plots showing a decrease in transmission of global radiation with increasing cloudiness had the highest ratios of proportion direct transmitted to proportion diffuse transmitted. In the most open plots extensive scattering of direct radiation on clear days would be reduced on cloudy days and the proportion of global transmitted may decrease. During winter with low solar elevation, penetration of direct radiation and downward scattering of direct beam are minimal because of the acute angle of the sun to tree crowns and increased albedo. On cloudy days then, the proportion of global transmitted may increase because diffuse radiation is entering through many canopy gaps. But for the same canopy transmitting appreciable direct radiation during summer, the proportion of global transmitted may decrease with increasing clouds. Lindroth and Perttu (1981) showed that transmission of global radiation decreased with decreasing solar altitude in a *Pinus sylvestris* L. stand. Slaughter (1983), though, found no consistent change in transmission with changes in cloud cover or solar altitude in a *Picea mariana* (Mill.) B.S.P. stand sampled during May-September.

In summary, the equations predicting the proportion of diffuse radiation transmitted that include direct beam scattering would change with increasing cloudiness and at different times of the year. Equations predicting the proportion of direct radiation transmitted would likely be affected by weather conditions and are highly dependent upon solar altitude. Adding a term to account for solar angle may broaden the generality of the equations, if relative gap frequency in the solar path among stands is assumed the same. Equations predicting transmission of global radiation are affected by the proportions of diffuse and direct radiation transmitted, cloud cover, and interaction with stand structure.

CONCLUSION

Although equations predicting transmission of radiation components may not give accurate estimates when used under different sky conditions, or solar altitudes, they do demonstrate the relationships between transmission and stand characteristics for a given time period under specific sky conditions. The results of other studies suggesting the use of sum of diameters to predict transmission of solar radiation are confirmed. Reineke's (1933) stand density index has merit as a predictor variable, and is an easily measured index that has not been used previously to predict transmission. Overstory cover is an apparently good integrator of inter-plot variation once HBLC's are above sensors, and is useful for predicting transmission of diffuse and diffuse photosynthetically active radiation. Extinction of diffuse radiation is best predicted using overstory cover as measured by a 10° angle moosehorn. Extinction of global and direct radiation following Beer's law is best predicted using sum of tree diameters or stand density index.

Equations predicting transmission of direct radiation did not differ between the two broad classes of stand structure. Stand structure affected transmission of diffuse radiation resulting in equation differences. Equation differences were equivocal for transmission of global and diffuse photosynthetic photon flux density, in part, because these two components were affected by transmission of diffuse radiation.

Hemispherical photographic estimates of transmission of diffuse, diffuse photosynthetic photon flux density, and direct radiation were significantly different from measured proportions transmitted.

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CHAPTER 4. RELATIONSHIPS OF SALAL (GAULTHERIA SHALLON) TO TRANSMISSION OF SOLAR RADIATION THROUGH FOREST CANOPIES

INTRODUCTION

Salal (Gaultheria shallon Pursh) is a forest understory species widely distributed along the Pacific Coast of North America. Despite its ubiquitous distribution in coastal forests, little work has been done on salal ecology. Sabhasri (1961) found that photosynthesis of salal plants under a forest canopy was 16% of those plants in the open and concluded that salal was an intolerant species. Swank (1972) concluded that salal sun plants were under greater moisture stress than shade plants. Stanek et al. (1979) reported that salal cover was positively related to diffuse photosynthetically active radiation below coniferous forest canopies. Foresters are concerned with salal because it competes with trees for soil moisture (Tan et al. 1977; Black et al. 1980) and possibly nutrients (Weetman et al. 1986).

Salal has two distinctly different growth forms. Shoots in open areas are numerous and short (Chapter 2), with thick (Swank 1972), small leaves (Kelliher 1985). Shoots under canopies and in shade are taller, with larger, darker green leaves. Because salal responds to small openings in a forest canopy with increased vigor (Vales and Bunnell 1986) and is related to levels of forest stocking (Long and Turner 1975; Chapter 2), light seems to be an important factor in salal growth.

Studies of forest understory growth have shown a positive relationship with light transmission (e.g., Zavitkovski 1976). Anderson et al. (1969) also found that understory abundance was positively correlated with light transmission but that the understory was more responsive to throughfall precipitation than to light transmission. Interactions between light and moisture are probably important (Atzet and Waring 1970).

Direct radiation under forest canopies in the form of sunflecks may result in increased photosynthesis (e.g., Shirley 1945; Gross and Chabot 1979; Gross 1982), influence photosynthesis (Hodges 1967), influence moisture status and distribution of plants (Young and Smith 1979; Ustin et al. 1984), or have little effect on plants (Logan 1959). Sunflecks contribute significantly to the radiation regime below a forest canopy (Evans 1956; Czarnowski and Slomka 1959; Miller 1959; Muller 1971) and are additive to diffuse radiation (Federer and Tanner 1966).

This study examined the relationship of salal abundance and shoot size to transmission of components of solar radiation through forest canopies. Specific objectives were to: (1) explore the form of the relationship of salal density, basal area, productivity, biomass, cover, and shoot size to transmission of global, direct, diffuse, and diffuse photosynthetically active (measured as photon flux density, PPFD) solar radiation; (2) evaluate if the relationships differed between stand structures and biogeoclimatic subzones; and (3) evaluate which solar radiation component may be the most important for regulating salal growth.

STUDY AREAS

Twelve plots were sampled at several locations on Vancouver Island, British Columbia, Canada. Six plots were in the Coastal Western Hemlock dry subzone (CWHa; Krajina 1965) and 6 were in the CWH wet subzone (CWHb). Plots in the CWHa were in the *Gaultheria* - western hemlock - Douglas-fir plant association (Orloci 1965) and CWHb plots were in the *Vaccinium* - *Gaultheria* - western hemlock - Douglas-fir plant association (Orloci 1965). The CWHa plots were separated geographically and in stands of different ages and structures. CWHb plots were all located in the same stand and separated by less than 800 m. The CWHb stand was younger, with smaller trees than most stands sampled in the CWHa. Soils were Humo-Ferric Podzols on morainal or colluvial veneer. Average annual precipitation is 2123 mm in the CWHa and about 2350 mm in the CWHb (Klinka et al. 1984).

All plots were in immature stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn). Additional tree species found in the CWHb stand were amabilis fir (*Abies amabilis* (Dougl.) Forbes), yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), and western white pine (*Pinus monticola* Dougl.). Understory species were primarily salal, red huckleberry (*Vaccinium parvifolium* Smith), and Oregon grape (*Mahonia nervosa* Pursh).

Plots were selected to encompass a range of overstory cover and salal abundances. Criteria used to locate plots were: homogeneous forest canopy structure, no deciduous trees, stand age 30-60 years, no stand treatment (e.g., no thinning or fertilization), slopes 10-60%, south-southwest aspects, and elevation 200-600 m. Descriptions of plots are given in Table 4.1.

TABLE 4.1 Descriptions of plots used to sample salal and solar radiation

Plot	Subzone	Aspect (°)	Elev. (m)	Slope (%)	Age	Cover[a]	BA (m^2/ha)
1	CWHa	230	430	30	28	0.912	37.7
2	CWHa	215	270	15	37	0.782	46.7
5	CWHa	206	310	52	60	0.636	35.0
6	CWHa	215	310	45	59	0.783	34.4
7	CWHa	173	200	9	34	0.345	14.8
9	CWHa	261	630	43	42	0.899	54.9
21	CWHb	240	570	30	30	0.576	10.1
22	CWHb	240	570	30	30	0.416	8.5
23	CWHb	220	570	20	30	0.809	41.6
24	CWHb	220	570	20	30	0.636	26.1
26	CWHb	219	550	19	30	0.902	38.9
27	CWHb	214	600	22	30	0.757	17.5

[a] Forest overstory cover estimated by moosehorn (Robinson 1947) as a proportion of 1.0.

METHODS

Detailed methods for sampling salal and solar radiation are given in Chapters 2 and 3. Briefly, salal was sampled in 52 0.25-m^2 quadrats systematically located within 9 x 25 m (0.0225 ha) plots with the long edge laid out along slope contours. Salal cover was visually estimated in each quadrat. All salal shoots rooted in the quadrat were counted, measured for basal diameter and height (distance from ground where rooted to top of previous year's growth when the shoot was pulled upright), and current growing season's leaves were counted. Total biomass of each shoot was estimated from allometric equations (Vales et al. in prep.) and did not include current annual growth (CAG) biomass. CAG foliar biomass was estimated by multiplying the number of CAG leaves by average leaf biomass obtained from a random sample of leaves after the growing season. Quadrat samples and shoot measurements were transformed to obtain normal distributions. Means and confidence intervals of transformed samples and shoot measurements are reported backtransformed. Estimates of density, basal area, and biomass are given as plot averages (n = 52/plot) and reported per m^2. Estimates of shoot height and basal diameter are plot averages of measurements of all shoots sampled in a plot.

Shortwave solar radiation (0.3-3.0 μm) was monitored with Dome solarimeters (Lintronic Ltd.) recorded on CR-21 data loggers as 3-minute averages of samples taken at 1-minute intervals. Shadow bands (Horowitz 1969) separated diffuse from global radiation with paired sensors on each stand mounted 1.5 m above ground. One pair of sensors recorded solar radiation in an open area near the plot to determine the amount of radiation potentially above the canopy. Two pairs of sensors were located 11 m apart within plots, along the centerline, and 7 m in from each edge. One LI-COR LI-190SB quantum sensor was shaded and used to monitor diffuse photosynthetic photon flux density radiation (PPFD; 0.4-0.7 μm) in the plot center as 3-minute averages of 1-minute samples. Diffuse open PPFD was empirically calculated from a calibration equation. Direct radiation was obtained by subtracting the diffuse radiation component from global radiation. Transmission of each component was computed by dividing the average daily sum of the two below-canopy sensors by the daily sum of open radiation. Only days that were clear were used for analyses. Each plot was monitored for at least one full day. Because variable weather conditions did not always permit monitoring a plot during one full clear day, half-day monitoring (sunrise to solar noon) was multiplied by 2 for two cases. Transmission was averaged for plots sampled over two days.

Regression equations were developed for salal abundances (density, DENSITY; basal area, SALALBA; foliar productivity, CAGBIOM; total biomass, TOTBIOM; and cover, PCTCOVER) as a function of transmission of each radiation component using the regression equation:

$$Y = \frac{a(X - c)}{1 + a(X-c)/b}$$

where Y is the salal variable, X is the proportion of a radiation component transmitted, a is the rate at which an asymptote is reached, b is the level of the asymptote, and c is the level of X where Y is 0. This form of the equation is a Michaelis-Menten type relationship and gives a form similar to the saturation curve of photosynthesis with increasing light intensity that is often used in modeling photosynthesis (Thornley 1976).

Parameter estimates were obtained using a nonlinear regression, derivative-free parameter-estimating FORTRAN subroutine (Moore 1984). Standard error of the estimate ($s_{y.x}$) and index of determination (i^2: Ezekiel and Fox 1970) were computed for each regression with a FORTRAN program.

RESULTS

Salal estimates ranged from 0.12-144.3 shoots$\cdot$m^{-2} for density, 0.01-14.0 cm$^2\cdot$m^{-2} for basal area, 0.06-634 g$\cdot$m^{-2} for biomass, 0.006-64.7 g$\cdot$m^{-2} for foliar productivity, 23-75 cm for average shoot height, and 0.26-0.54 cm for average shoot basal diameter (Table 4.2). Ranges of the proportions of radiation components transmitted were 0.026-0.57 for global, 0.18-1.80 for diffuse, 0.005-0.43 for direct, and 0.01-0.29 for diffuse PPFD (Table 4.3). The proportion of diffuse radiation included within-canopy scattering of direct beam and was not the true proportion of diffuse sky radiation transmitted. Stand structure in the CWHb caused some proportions of diffuse radiation transmitted to be greater than 1.0 (see Chapter 3). Daily maxima and average flux densities of solar radiation below the canopies are summarized (Table 4.3).

Form of Response

Salal abundances were closely related to proportions of the radiation components transmitted within and across subzones (Table 4.4). The response of all salal abundances to transmission of global, direct, and diffuse PPFD were nonlinear, increasing asymptotically (Figs. 4.1-4.3). The response of salal to transmission of diffuse radiation increased nonlinearly with either no or an unrealistically high upper asymptote (Figs. 4.1-4.3; Table 4.4). Diffuse irradiances under canopies were low (Table 4.3). When average daily irradiance of global and diffuse radiation below the canopy were about equal (e.g., global plot 1 and diffuse plot 5, plots 23 or 26 in Table 4.3) the proportion of diffuse transmitted was about 10x that of global.

Although salal showed an almost unlimited increase with transmission of diffuse radiation, salal apparently approached an asymptote with increasing proportion of diffuse PPFD transmitted (Table 4.4; Figs. 4.1-4.3). Below-canopy diffuse radiation was low in PPFD (Chapter 3) because of absorption by the forest canopy. The amount of PPFD in below-canopy diffuse radiation, however, increased with increasing proportion of PPFD transmitted (Chapter 3).

Salal Shoot Size

The relationship of salal shoot size (height and basal diameter) to transmission of global and direct radiation (Fig. 4.4) showed considerable variability in the CWHa, probably due to site and age differences. A slight relationship was found in the CWHb stand of the same age, despite a narrow range of shoot sizes. At the lowest transmission shoots were small. As transmission increased, shoot height and diameter were larger, but as transmission further increased, height and basal diameter decreased. The relationships were more pronounced for height than for basal diameter. Salal shoot size was adversely affected by high transmission of solar radiation. Shoots were productive, however, under open canopies with high transmittance (Fig. 4.5).

Subzone Differences

A qualitative assessment was made of potential differences of equations between subzones because no tests were available for the form of regression

TABLE 4.2 Plot means and 95% confidence intervals for salal characteristics

Plot	DENSITY $(\#\cdot m^{-2})$[a]		CAGBIOM $(g\cdot m^{-2})$[a]		TOTBIOM $(g\cdot m^{-2})$[a]		PCTCOVER (%)[b]		HEIGHT (cm)[c]			Basal dia. (cm)[c]	
	$\bar{x}$	Conf. int.	$\bar{x}$	Conf. int.	$\bar{x}$	Conf. int.	$\bar{x}$	Conf. int.	$\bar{x}$	Conf. int.	n	$\bar{x}$	Conf. int.
1	0.7	0.1- 1.7	0.02	0.0- 0.1	0.23	0.0- 1.0	0.4	0.1- 1.0	25.3	18.9-32.5	44	0.21	0.28-0.24
2	10.8	6.9- 15.7	2.13	1.0- 3.9	20.07	10.0- 35.2	9.6	6.2-13.6	23.8	21.1-26.6	209	0.26	0.24-0.28
5	28.2	23.6- 33.2	28.13	20.0-38.2	271.07	189.4-373.3	51.1	43.8-59.0	47.2	43.4-51.1	354	0.39	0.37-0.41
6	16.5	12.8- 20.6	25.56	15.1-39.9	400.28	242.9-614.0	38.5	32.8-44.6	74.8	67.5-82.6	237	0.54	0.49-0.59
7	68.0	57.2- 79.8	64.65	50.4-81.4	633.57	466.9-835.8	50.3	43.5-57.6	43.1	40.9-45.4	881	0.41	0,39-0.42
9	0.1	0.0- 0.4	0.01	0.0- 0.0	0.06	0.0- 0.3	0.1	0.0- 0.2	34.8	24.0-47.5	12	0.34	0.26-0.44
21	102.1	85.5-120.6	36.48	30.9-42.7	278.07	211.9-356.7	52.9	45.7-60.5	27.2	26.1-28.3	1294	0.30	0.29-0.30
22	144.5	124.9-165.5	55.59	45.8-66.6	289.17	216.7-376.1	48.7	40.4-57.7	22.6	21.8-23.4	1750	0.31	0.31-0.32
23	12.7	8.6- 17.7	3.33	1.8- 5.5	92.61	46.3-162.4	12.2	7.7-17.8	43.3	37.9-49.1	209	0.37	0.35-0.40
24	50.4	37.9- 64.8	19.38	13.6-26.5	165.15	105.6-243.6	33.5	25.8-42.3	32.3	30.5-34.1	680	0.30	0.29-0.31
26	5.7	2.9- 9.3	0.58	0.2- 1.2	7.22	2.6- 15.3	2.6	1.2- 4.5	24.3	20.8-28.0	126	0.27	0.25-0.30
27	40.0	29.2- 52.5	13.99	8.9-20.8	226.96	139.3-345.2	26.6	20.6-33.4	43.9	41.6-46.2	608	0.34	0.33-0.35

[a] Average of 52 0.25m² quadrats x 4.

[b] Average of 52 0.25m² quadrats.

[c] Average of all shoots measured. See *n* for sample sizes.

TABLE 4.3 Below-canopy solar radiation statistics

Plot	GLOBAL			DIRECT			DIFFUSE			PPFD[a]		
	Max (W·m^{-2})	$\bar{x}$	P.T.[b]	Max (W·m^{-2})	$\bar{x}$	P.T.	Max (W·m^{-2})	$\bar{x}$	P.T.	Max (μE·m^{-2}·s^{-1})	$\bar{x}$	P.T.
1[c]	90	15	0.026	75	4	0.008	26	10	0.177	5	1.6	0.010
2	810	35	0.074	779	23	0.053	33	12	0.360	9	4.5	0.050
5[d]	720	31	0.073	676	16	0.046	64	16	0.260	35	11.9	0.069
6	750	41	0.091	710	22	0.058	43	19	0.286	40	15.9	0.088
7[e]	940	200	0.465	860	165	0.429	96	35	0.775	104	43.1	0.286
9[c]	600	20	0.040	579	6	0.013	34	14	0.310	9	1.4	0.011
21	890	129	0.277	690	54	0.127	215	75	1.429	98	38.3	0.261
22	990	250	0.566	846	164	0.416	165	86	1.799	66	28.7	0.216
23[c]	120	27	0.058	78	96	0.006	65	24	0.569	9	4.3	0.036
24	350	62	0.135	272	15	0.035	140	47	1.153	26	12.7	0.112
26	100	17	0.035	84	2	0.005	30	15	0.338	4	2.0	0.016
27	560	65	0.142	438	17	0.039	120	48	1.293	21	8.3	0.080

[a] Diffuse photosynthetic photon flux density.

[b] Proportion of above-canopy radiation transmitted.

[c] Average of monitoring for two days.

[d] Computed from monitoring one full day and one half-day.

[e] Computed from monitoring one half-day.

TABLE 4.4 Regression coefficients of equations predicting salal variables from solar radiation components. Sample sizes: CWHa=6, CWHb=6. Equations significant at $p < 0.06$. Regression equation: $Y = \frac{a(X-c)}{1 + a(X-c)/b}$

Y	Subzone	X	a	b	c	r^2	$s_{y \cdot x}$
DENSITY:	CWHa	GLOBAL	418.8	108.1	0.0290	0.93	7.5
		DIRECT	495.5	100.6	0.0083	0.93	7.4
		DIFFUSE	1.3	-3.4	-1.7280	0.83	11.7
		PPFD	324.0	273.7	0.0081	0.95	6.1
	CWHb	GLOBAL	559.4	288.9	0.0315	0.98	7.5
		DIRECT	1686.3	183.5	-0.0002	0.99	5.8
		DIFFUSE	35.5	-87.1	0.2575	0.93	16.4
		PPFD	776.6	369.9	0.0164	0.87	22.2
	Both	GLOBAL	520.9	211.1	0.0317	0.86	17.9
		DIRECT	1054.[illegible]	146.0	0.0033	0.71	25.3
		DIFFUSE	72.9	221167.7	0.1811	0.80	21.2
		PPFD	682.0	246.6	0.0163	0.76	23.2
SALALBA:	CWHa	GLOBAL	122.8	19.3	0.0324	0.88	2.2
		DIRECT	140.7	18.4	0.0104	0.85	2.4
		DIFFUSE	0.2	-0.6	-2.5214	0.69	3.5
		PPFD	103.3	28.6	0.0139	0.94	1.5
	CWHb	GLOBAL	53.4	24.2	0.0255	0.99	0.3
		DIRECT	159.5	16.2	-0.0027	0.99	0.5
		DIFFUSE	3.1	-8.1	0.1737	0.96	1.1
		PPFD	80.7	24.8	0.0127	0.85	2.1
	Both	GLOBAL	71.0	21.3	0.0257	0.89	1.7
		DIRECT	134.4	17.9	0.0020	0.89	1.7
		DIFFUSE	5.7	8804.0	-0.1711	0.40	4.0
		PPFD	87.2	27.2	0.0127	0.88	1.8
TOTBIOM:	CWHa	GLOBAL	6631.0	829.5	0.0325	0.82	125.7
		DIRECT	7730.0	790.7	0.0106	0.79	135.2
		DIFFUSE	N.S.[a]				
		PPFD	5665.0	1119.3	0.0141	0.90	91.9
	CWHb	GLOBAL	4758.0	337.3	0.0330	0.97	22.7
		DIRECT	16027.0	309.1	0.0016	0.92	34.5
		DIFFUSE	196.6	-547155.	0.1992	0.94	29.2
		PPFD	6241.0	343.5	0.0151	0.92	35.3
	Both	GLOBAL	5277.0	497.8	0.0307	0.60	128.4
		DIRECT	7405.0	531.7	0.0027	0.63	122.4
		DIFFUSE	N.S.				
		PPFD	4679.0	655.3	0.0123	0.68	114.8
CAGBIOM:	CWHa	GLOBAL	476.8	94.6	0.0320	0.88	9.9
		DIRECT	537.2	90.6	0.0098	0.86	10.6
		DIFFUSE	0.6	-2.3	-2.6543	0.73	14.6
		PPFD	406.1	157.8	0.0139	0.94	7.1
	CWHb	GLOBAL	204.6	116.5	0.0374	0.99	2.6
		DIRECT	603.2	71.3	0.0016	0.99	2.6
		DIFFUSE	14.4	-33.2	0.3522	0.94	5.9
		PPFD	317.6	120.7	0.0219	0.84	9.3
	Both	GLOBAL	245.3	113.1	0.0254	0.86	8.7
		DIRECT	523.7	82.9	0.0044	0.90	7.4
		DIFFUSE	23.3	899135.0	-0.1637	0.33	19.0
		PPFD	317.5	162.3	0.0148	0.86	8.7
PCTCOVER:	CWHa	GLOBAL	1245.0	58.6	0.0294	0.64	16.3
		DIRECT	1879.0	53.9	0.0098	0.65	16.0
		DIFFUSE	N.S.				
		PPFD	1202.0	63.6	0.0111	0.79	12.5
	CWHb	GLOBAL	620.1	62.9	0.0318	0.93	5.7
		DIRECT	2096.0	55.8	0.0013	0.93	5.9
		DIFFUSE	44.5	210.6	0.2818	0.87	8.0
		PPFD	557.8	84.9	0.0113	0.99	0.2
	Both	GLOBAL	984.5	56.9	0.0303	0.73	11.6
		DIRECT	1651.0	56.6	0.0040	0.72	11.8
		DIFFUSE	N.S.				
		PPFD	905.3	66.7	0.0121	0.85	8.7

[a] Equation not significant ($p \geq 0.06$).

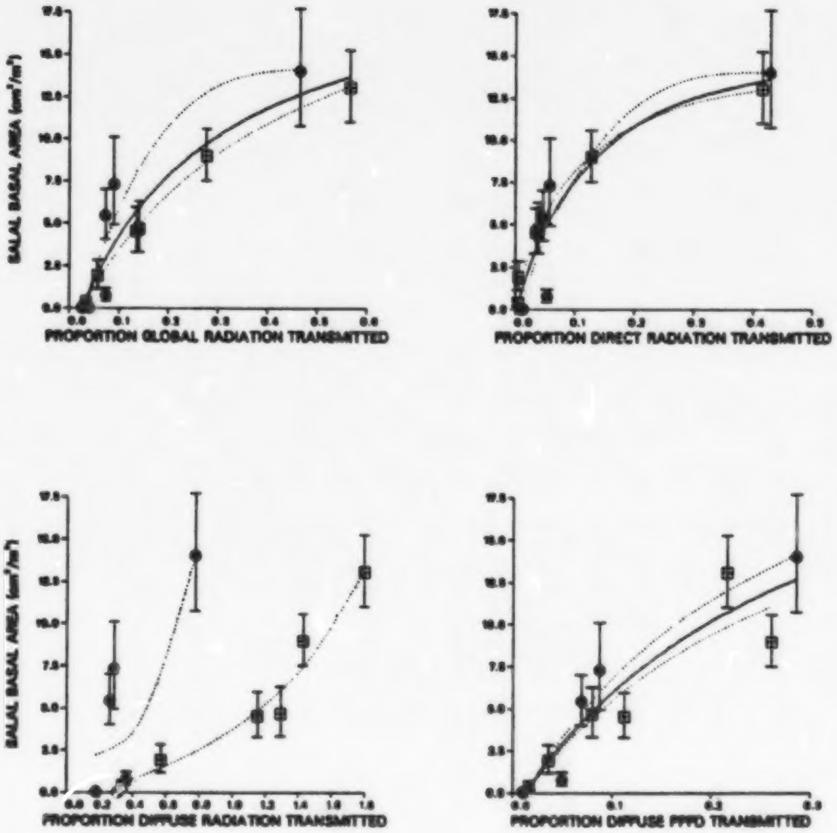

Figure 4.1. Relationships of salal basal area (cm^2·m^{-2}) and 95% confidence intervals to transmission of global, direct, diffuse, and diffuse PPFD solar radiation components. Dotted lines are relationships in individual subzones. CWHa (•), CWHb (⊞).

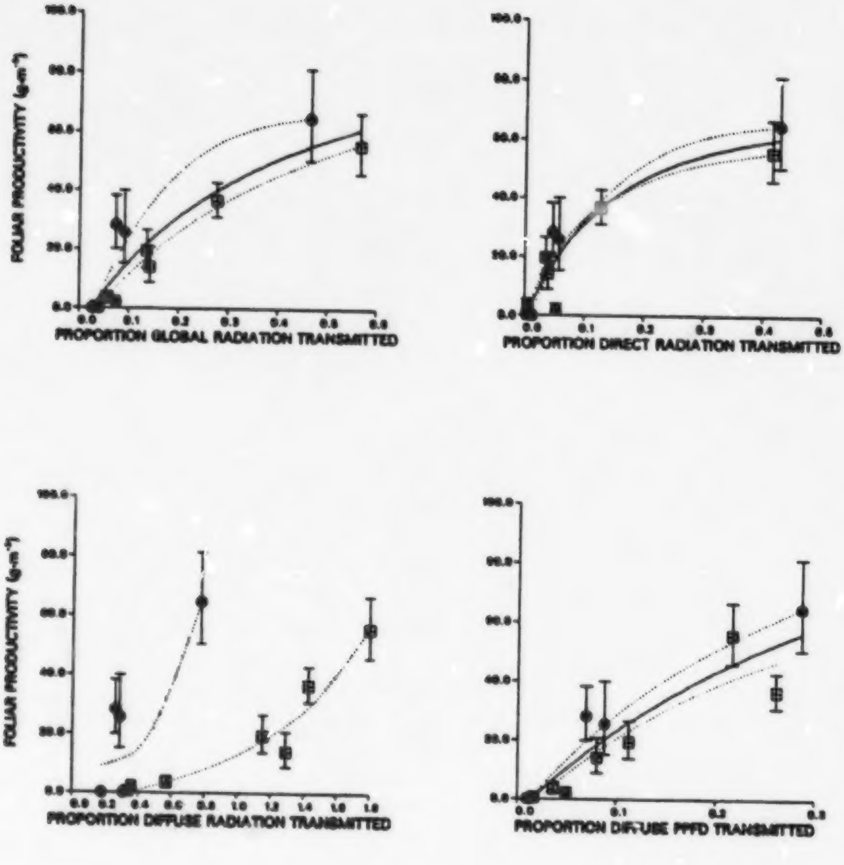

Figure 4.2. Relationships of salal foliar productivity ($g \cdot m^{-2}$; CAGBIOM) and 95% confidence intervals to transmission of global, direct, diffuse, and diffuse PPFD solar radiation components. Dotted lines are relationships in individual subzones. CWHa (●), CWHb (⊞).

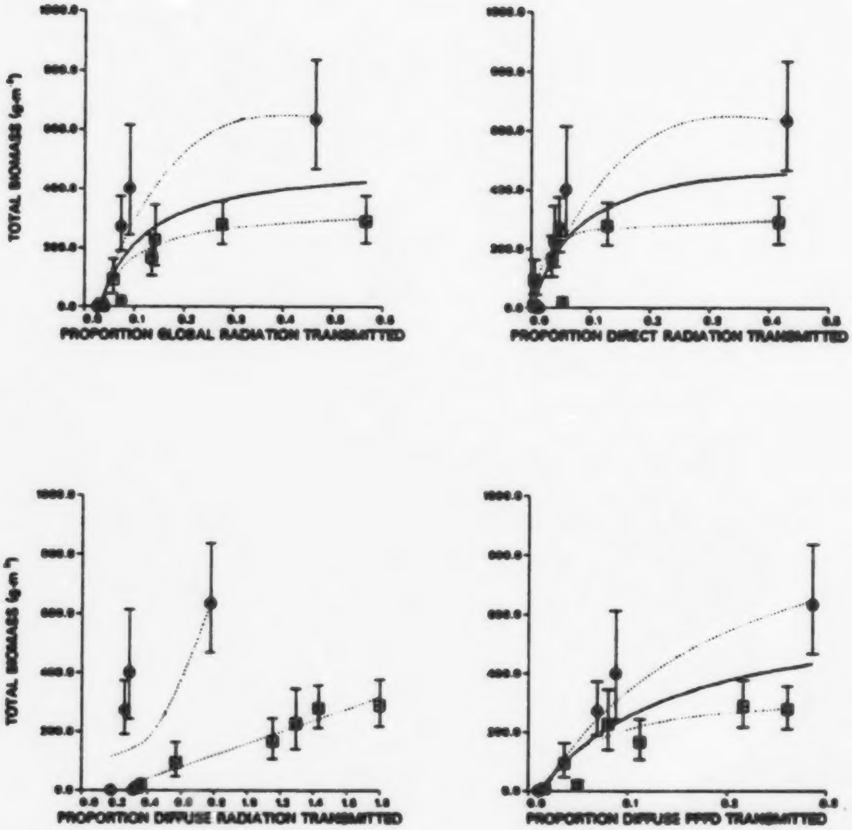

Figure 4.3. Relationships of salal total biomass ($g\cdot m^{-2}$; TOTBIOM) and 95% confidence intervals to transmission of global, direct, diffuse, and diffuse PPFD solar radiation components. Dotted lines are relationships in individual subzones. CWHa (•), CWHb (⊞).

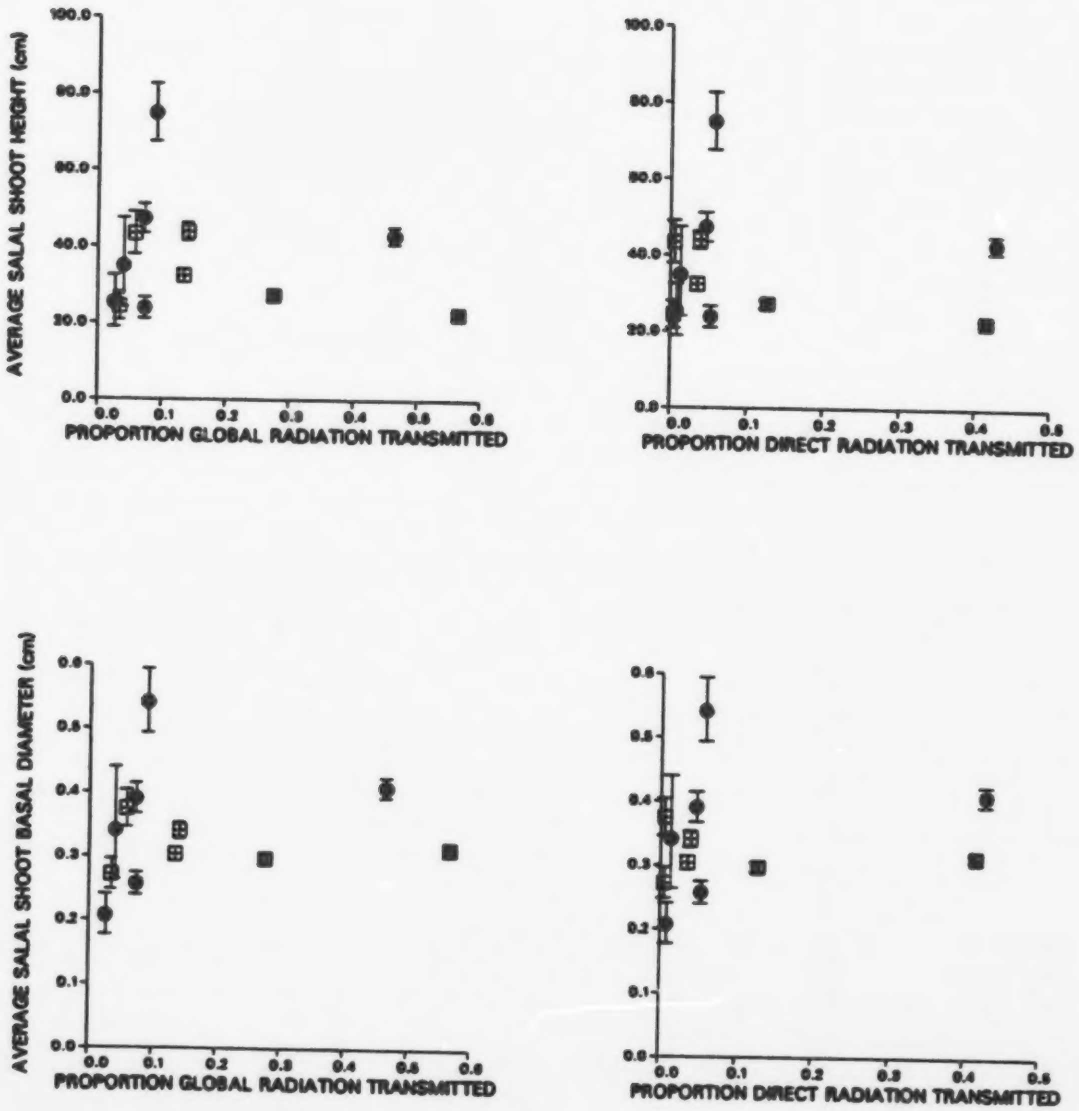

Figure 4.4. Relationships of average shoot height (cm) and basal diameter (cm) of salal with 95% confidence intervals to transmission of global and direct radiation. CWHa (•), CWHb (⊞).

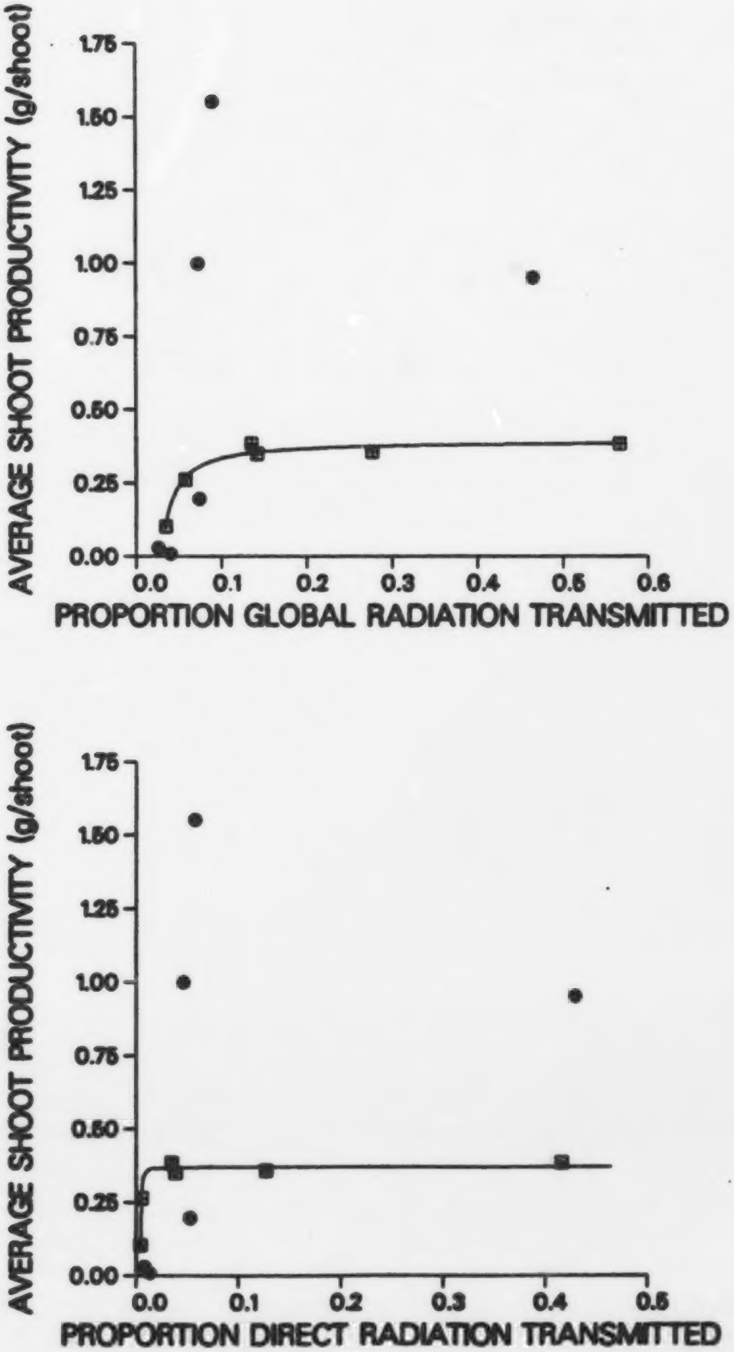

Figure 4.5. Relationships of average productivity of salal shoots to transmission of global and direct solar radiation. CWHa (•), CWHb (⊞).

equation used. Equations differed strongly in all cases where salal was predicted by diffuse radiation (e.g., Figs. 4.1-4.3; Table 4.4). Differences between the equations were due to differences in stand structure between the subzones and the different way in which diffuse radiation was transmitted (see Chapter 3 Fig. 3.2). Any site effects that would have contributed to differences in salal between the subzones were masked by the differential transmission of diffuse radiation between the two stand structures.

The manner in which radiation is transmitted by different stand structures and the effects of stand age and site quality interact to affect regression coefficients. Among stands, maximum abundance of salal for a given proportion of radiation transmitted would likely be regulated by site and age effects. The rate at which a maximum is reached (coefficient a) and upper asymptote (coefficient b) are regulated by an interaction of the way in which radiation is transmitted (stand structures) and site and age effects. Although differences between subzones are discussed, the potential subzone effects that might cause equations to be different are confounded by broad differences in stand structure and transmission between the two subzones.

Equations predicting salal density and total biomass per unit area from transmission of global, direct and diffuse PPFD radiation differed between subzones (e.g., Fig. 4.3; Table 4.4). Maximum density was considerably lower in the CWHa than in the CWHb and maximum total biomass was much greater in the CWHa. Slopes (coefficient a) also differed strongly (Table 4.4). Site and age effects resulted in a lower density (Table 4.4) of larger shoots (Fig. 4.4) in the CWHa. Because individual shoot biomass is allometrically related to shoot size, a small change in shoot size would give a proportionately greater change in shoot biomass. Although plot 7 density was less than one-half that of plot 22's (Table 4.2), average shoot biomass in plot 7 was more than quadruple that of shoots in plot 22.

Differences in equations predicting salal basal area, foliar productivity, and percent cover from transmission of global, direct, and diffuse PPFD radiation were less pronounced. The subzone having the largest coefficient b for SALALBA and CAGBIOM and greatest magnitude of difference of coefficient a differed among the radiation components. Equations predicting SALALBA, CAGBIOM, and PCTCOVER from the proportion of direct radiation transmitted generally did not differ. Transmission of direct radiation did not differ between the subzones (Chapter 3). Although individual shoot productivity and basal area in the CWHa plot 7 was about twice that of CWHb plot 22 (Fig. 4.5), density was about one-half and therefore SALALBA and CAGBIOM per unit area were similar in the two subzones (Table 4.2; Figs. 4.1 and 4.2). Because transmission of direct radiation between the stand structures and salal abundance were similar, equations did not differ. Equations predicting SALALBA, CAGBIOM, and PCTCOVER from the proportion of global and diffuse PPFD radiation appeared to differ (e.g., Figs. 4.1 and 4.2), likely due, in part, to potential differences in the way these radiation components were transmitted (Chapter 3). Additionally, global and diffuse PPFD contain diffuse radiation which was transmitted very differently by the two stand structures.

The form of the relationships of salal shoot size (Fig. 4.4) and shoot productivity (Fig. 4.5) to transmission of radiation did not differ substantially between subzones. Absolute values for a given proportion transmitted differed probably because of site and age effects.

Relative Predictability Among Radiation Components

Although transmission of diffuse radiation would predict unrealistically high regression estimates of salal abundance at proportions transmitted beyond what was found here, transmission of diffuse radiation did adequately predict salal abundance in the CWHb (i^2 = 0.87-0.96). Relationships using diffuse radiation in the CWHa were poorer than using other components. Results between the subzones differed, with PPFD predicting all salal abundances better than other components in the CWHa, but PPFD generally had a lower predictability than other components in the CWHb. Transmission of PPFD was more closely related to forest stand characteristics in the CWHa than in the CWHb (Chapter 3 Table 3.3). Salal abundances were better predicted by transmission of global and direct radiation in the CWHb than in the CWHa even though transmission of global and direct radiation were better predicted by stand characteristics in the CWHa (Chapter 3 Tables 3.3 and 3.4). The lack of site variation in the CWHb may have contributed to the better predictabilities. SALALBA, CAGBIOM, and PCTCOVER were predicted about equally well by global and direct radiation for combined equations. Density, total biomass, and cover also were predicted about equally well by transmission of global and direct radiation in individual subzones.

Effects of Radiation Components on Salal

Salal abundances consistently reached upper asymptotes faster for transmission of direct radiation than for other components (coefficient a, Table 4.4; Figs. 4.1-4.3). Salal maxima were consistently lower for transmission of direct radiation (coefficient b, Table 4.4), and the proportion of direct radiation transmitted at levels of salal near zero was generally less than for global or PPFD (coefficient c, Table 4.4). These results suggest that salal is more closely regulated by transmission of the direct radiation component than by other components.

DISCUSSION

Salal density, basal area, biomass, productivity per shoot and per unit area, and cover increased asymptotically with increasing proportions of global, direct, and diffuse photosynthetic photon flux density radiation (Figs. 4.1-4.3, 4.5). The forms of the relationships were similar to the asymptotic relationship of photosynthetic response to light intensity. Because diffuse irradiance below canopies was low, the relationships of salal abundances to transmission of diffuse radiation were in the lower phase of the saturation curve. The difference between diffuse PPFD and diffuse shortwave relationships demonstrate the importance of measuring photon flux as opposed to relating understory plant growth to diffuse shortwave solar energy below a canopy.

The interaction of solar radiation and its influence on moisture relations in salal was demonstrated by Swank (1972). He concluded that salal "sun" plants were under greater water stress for a longer time than shade plants. Of three light intensities used in a greenhouse experiment (400, 1600, 2600 f.c.), Swank (1972) found salal photosynthesis to be greatest under the mid-light intensity. Light intensity under canopies on sunny days in summer is usually less than 2000 f.c. The combination of high light intensity and greater water stress resulted in lowered net photosynthetic rate for "sun" plants compared to "shade" plants. The results in this study indicated that shoots that received a high proportion of direct radiation were smaller (possibly because of lowered photosynthetic rate or moisture stress) than shoots that received less radiation (Fig. 4.4). Shoot productivity, however, increased asymptotically (Fig. 4.5). At low light intensity, Swank (1972) reported that photosynthesis was lowest. Results here found that shoots that received the lowest proportion of radiation transmitted were smaller and less productive than shoots that received more radiation, likely because there was too little light for adequate growth.

My results are also consistent with the ideas of Whitehead (1973). He discussed "compensation" by plants growing in low light environments. Plants compensate for low light by allocating assimilates to leaf material, increasing leaf size to increase the area of photosynthetic tissue, and thus ensuring that the same amount of carbon is fixed per unit time as plants receiving more light. An expense is paid for compensation by reduced reproductive structures. Sabhasri (1961) and Bunnell and Koch-Bakker (1986) found that salal shoots have more flowers in open areas than under forest canopies. Data are not available on salal reproduction by rhizomes in open areas and under canopies. Salal recruitment as measured by determining salal population age structure was greater in open, young clearcut areas than under old-growth forest canopies (R.M. Ellis, unpubl. data, B.C. Ministry of Forests, Victoria, B.C.). Bunnell and Koch-Bakker (1986) found salal "plants" in open areas had more shoots than "plants" under canopies, even though canopy plants were older.

Boardman (1977) reviewed physiological differences between sun and shade plants. He stated that shade plants generally have lower light saturation and compensation levels, lower dark respiration rates, are richer in chlorophyll, have lower stomatal density, and thinner leaves. Sun plants with thicker leaves and higher density of stomata have higher conductances to CO_2 diffusion and consequently greater CO_2 fixation. Swank (1972) found that salal leaves from sun plants were thicker than shade plants, consistent with Boardman (1977). Sabhasri (1961) reported that salal sun plant leaves had a higher mass per unit surface area than shade plant leaves. Kelliher (1985) found salal leaf size to increase with increasing stand basal area (reduced proportion of radiation transmitted, Chapter 3), consistent with Whitehead's (1973) observations. The relationship betwen my salal average leaf masses by plot and proportions of radiation transmitted had a pronounced form of relationship similar to that between shoot height and proportions transmitted. Salal leaves in shade are darker green than in open areas. Although not examined in this study, it is likely that salal sun and shade plants have a physiology consistent with the species reviewed by Boardman (1977).

A possible additional explanation for taller shoots under low to moderate proportions transmitted could be due to the effects of near infra-red wavelengths (NIR) on stem elongation. Sabhasri (1961) found that salal shoot length was greatest under red light. The spectral composition below a coniferous forest canopy is rich in NIR (Federer and Tanner 1966) and may stimulate stem elongation. Evans (1973) also mentioned that etiolation caused stem elongation in older shoots at low light intensities. It is unclear whether "compensation", moisture stress, photosynthetic rate, or NIR enrichment alone can explain the differences in shoot size among different proportions transmitted.

Although salal shoot size and biomass per shoot were smaller at the highest proportions of radiation transmitted (Fig. 4.4), foliar productivity per shoot increased (Fig. 4.5). The rate of increase is most rapid with a small increase in the proportion of direct radiation transmitted. Apparently shoots in the open do not accumulate much biomass, either losing their leaves rapidly or having twigs dying back. Leaves may die back early because of high moisture stress (Swank 1972). Because open-grown salal is productive, assimilates may be allocated to production of flowers and fruit (Sabhasri 1961; Bunnell and Koch-Bakker 1986) or reproduction by rhizomes (Bunnell and Koch-Bakker 1986; R.M. Ellis, unpubl. data) resulting in high shoot density. Sabhasri (1961) found that root length was greatest at the highest light intensity he used (400 f.c.).

Increases in salal abundance per unit area were found with increased proportions transmitted. Within a subzone the greater density of shoots under open canopies compensated for smaller shoots to give an overall increase in basal area and biomass. Shoot density in open areas may be high because of increased reproduction (Whitehead 1973) as was found by Bunnell and Koch-Bakker (1986) and Ellis (unpubl. data), or reduced competition for light among shoots. Fewer shoots are found under denser canopies, possibly because intra-specific competition causes thinning, or because lower proportion of radiation transmitted is associated with higher stand densities (Chapter 3), and potential inter-specific competition with trees for moisture (Black et al. 1980) or possibly nutrients (Weetman et al. 1986).

Apparent differences between equations developed in individual subzones could be attributed to the way radiation was transmitted by different stand structures (Chapter 3) and site and age differences. Equations differed strongly with diffuse radiation as an independent variable, and all equations differed with density and total biomass as dependent variables. Within a stand, density and biomass are affected by an interaction of solar radiation (Table 4.4) and stand density (Chapter 2). Among stands, as between the CWHa and CWHb, and within the CWHa, maximum biomass and density may differ for a given proportion of radiation transmitted or stand density, either because of age differences, nutrition (e.g., Keyes and Grier 1981), or site water balance (Grier and Running 1977; Gholz 1982). Wetter salal sites on the west and north coast of Vancouver Island support much larger shoots than are found on the drier interior and eastern parts of the Island.

Subzone differences were slightly evident for salal basal area, productivity, or cover predicted from transmission of global or diffuse PPFD. Only direct radiation showed no pronounced difference between subzones for relationships predicting salal basal area, foliar productivity, or cover.

All salal variables were predicted well by most radiation components (Table 4.4). Transmission of direct radiation had the most influence on salal (maxima lowest and rate of increase fastest). Because the below-canopy diffuse radiation was low in photon flux (Chapter 3), sunflecks would likely contribute significantly to the total PPFD below a canopy. Gross (1982) stated that the closer the average low light level is to a plant's compensation point, the more important sunflecks become. The steep slopes (coefficient a) of the equations predicting salal from direct radiation support Gross' (1982) statement. My results suggest that salal density, biomass and shoot size are likely regulated by an interaction of direct radiation, and probably with plant age and moisture status, and effects of site age (successional stage) and water balance.

CONCLUSION

Salal density, productivity, biomass, cover, and shoot size were well related to transmission of solar radiation through forest canopies. Relationships between salal abundance and transmission of global, direct, and diffuse photosynthetically active radiation were asymptotic. Differences between equations developed in different subzones were a function of stand structure effects on transmission of radiation and site effects. Salal density, productivity, biomass, and cover were most responsive to transmission of direct shortwave solar radiation.

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CHAPTER 5. MANAGEMENT IMPLICATIONS

INTRODUCTION

The results of this thesis can serve two useful purposes for managers. Forest managers concerned with competition by salal for moisture or nutrients can identify a level of MCC or stocking that is high enough to suppress salal. Wildlife managers interested in producing salal as winter forage can suggest levels of forest stocking that are optimum for salal height and productivity. Salal abundance can be predicted from forest inventories (e.g., timber cruise data) on sites similar to those sampled in this study. Equations predicting transmission of solar radiation may aid in modeling the deer thermal environment under forest canopies (Bunnell et al. 1986), but because of spatial heterogeneity and seasonal variation of the radiation regime, the equations in Chapter 3 must be used with caution. The results of the previous three chapters will be integrated along with additional material from published literature to illustrate how results from previous chapters can be applied.

FOREST MANAGEMENT IMPLICATIONS

Tan et al. (1977), Black et al. (1980), Kelliher (1985), and Price et al. (1986) have shown that salal is a serious competitor with Douglas-fir trees for soil moisture on dry sites, and can reduce potential tree growth. Weetman et al. (1986) have suggested that salal may be a serious competitor for nitrogen and phosphorus contributing to "growth check" in Sitka spruce (Picea sitchensis (Bong.) Carr.) plantations on Vancouver Island oligotrophic peat sites.

Attaining rapid crown closure and maintaining high stand densities are suggested techniques to effectively "control" salal. Black and Spittlehouse (1981) recommended stand densities greater than 1500 trees$\cdot$ha^{-1}, depending on average soil water potential, to maintain high crown closure and suppress salal. Their estimate was based on a 25-year old Douglas-fir stand. Because stands are dynamic, the number of trees needed depends on age and size of the trees.

Reineke's (1933) stand density index (SDI) can be used to guide stocking levels for salal suppression. SDI is not dependent on site quality or age. Stand density management diagrams (Drew and Flewelling 1979) can guide planting and thinning densities throughout a rotation. An SDI that effectively controls salal can be maintained. If plots from this study are located on the stand density diagram of Drew and Flewelling (1979:523), all plots except 3, 7, 21, and 22 fall above the crown closure line. Plots 9, and 13-15 are above their "lower limit of the zone of imminent competition-mortality". Plots near or above the competition line have salal densities less than 15 shoots$\cdot$m^{-2}. An optimum management regime to control salal on dry Douglas-fir sites might be to maintain stands near or above the lower limit of the zone of imminent competition-mortality. Stand densities at this zone, however, would be experiencing inter-tree competition and thus negatively affect potential tree growth. The lower zone roughly corresponds to an SDI of 1200. Maintaining an SDI of 1200 would require higher planting and residual thinning densities than those normally used (densities given in Nyberg 1985). The number of trees required to maintain the 1200 SDI could be calculated at any point in time by: $\#\text{trees}\cdot\text{ha}^{-1} = 1200/(\text{DBH}_g/25)^{1.6}$ (Long 1985). The number of trees needed to maintain SDI's of 600, 800, 1000, and 1200 at different diameters are presented in Table 5.1. As seen in Table 5.1, the extraordinarily high tree densities are not practical for operational forest management regimes using Douglas-fir.

The salal density at which little or no competition occurs with forest trees is not known. Black and Spittlehous (1981) modeled the water balance to suggest stand densities needed to suppress salal. Tan et al. (1977) reported that salal stomatal closure began at a photon flux density of 250-350 μE$\cdot$m$^{-2}\cdot$s^{-1}. Osberg (1986) suggested that stands be dense enough to keep below-canopy energy flux densities under 20 W$\cdot$m^{-2}, thus effectively reducing understory evapotranspiration rate. On clear, sunny summer days the solar irradiance above a canopy can range 800-1000 W$\cdot$m^{-2}. Using Osberg's (1986) recommended 20 W$\cdot$m^{-2}, and a maximum 900 W$\cdot$m^{-2} above-canopy global irradiance, transmission of global radiation would be about 2%. Coefficient c in Chapter 4 equations (Table 4.4) suggested that at 3% transmission of global radiation salal density would be zero. Working back through the equation in Chapter 3

TABLE 5.1 Tree densities needed to maintain a constant stand density index as average diameter changes

DBH_q^a	# Trees/ha for SDI:[b]			
(cm)	600	800	1000	1200
2	34135	45514	56892	68271
4	11261	15014	18768	22521
6	5886	7848	9810	11772
8	3715	4953	6191	7429
10	2599	3466	4332	5199
12	1942	2589	3236	3883
14	1517	2023	2529	3034
16	1225	1634	2042	2451
18	1015	1353	1691	2030
20	857	1143	1429	1715
22	736	982	1227	1472
24	640	854	1067	1281
26	564	751	939	1127
28	500	667	834	1001
30	448	598	747	896
32	404	539	674	808
34	367	489	611	734
36	335	446	558	670
38	307	409	512	614
40	283	377	471	566
42	262	349	436	523
44	243	324	405	486
46	226	302	377	452
48	211	282	352	423
50	198	264	330	396

[a] Diameter of tree of average basal area.

[b] Reineke's stand density index.

combined gives an estimated SDI of 1065 at 2% transmission and 984 at 3%. Stands having an SDI greater than 1000 would likely have an adverse effect on salal, but site effects or sidelighting may support higher abundances than expected.

Crown closure is conventionally defined by foresters as the time when crowns begin to touch and cover the entire growing area. It is a useful measure of stand that is independent of age. Overstory cover as measured by the moosehorn is a measure of crown completeness, or an estimate of tree foliage density and is analogous to a cover estimate of an understory species. When tree crowns are overlapping, there is 100% crown closure, but this may correspond roughly to only 70% mean crown completeness. Crown completeness is a useful concept in research because it is a surrogate for processes acting below the canopy (light transmission or throughfall precipitation). Crown completeness as measured with a moosehorn, however, may not be as operationally practical as using aerial photographs to estimate crown closure. Bonnor (1968) related measurements made with the moosehorn to cover estimates obtained from aerial photos. He found that estimates made from the ground were about 10% higher than his estimates made from aerial photographs. Relationships between MCC and stand characteristics for a given level of stocking can be developed and used if MCC is the desired independent variable to use to predict salal.

WILDLIFE MANAGEMENT IMPLICATIONS

Because salal is an important winter food for black-tailed deer (Cowan 1945; Brown 1961; Rochelle 1980), managers may want to encourage forage production on deer winter ranges by manipulating forest stands (e.g., Nyberg et al. 1986). Medium site stands on southern aspects were studied to avoid developing prescriptions for salal production on good forest sites and potential conflicts with forest growth objectives.

Because extensive homogeneous cover of salal was not found during plot selection, and salal patches are usually spatially heterogeneous, single prescriptions over a large area to maintain a level of MCC may not yield results predicted from the regressions presented here. Exploiting natural openings and forage patches (Nyberg et al. 1986) in small areas may provide predictable responses in small patches. Because biomass relationships are generally hyperbolic, a small change in MCC will result in a proportionately larger change in forage production or biomass.

Management of salal as a single winter forage species may be unwise because a mixed diet seems to aid digestion (e.g., Rochelle 1980). Arboreal lichen (*Alectoria sarmentosa*) may increase the digestibility of salal (Rochelle 1980). Brown (1961) reported feeding trials lasting 30, 40, 41, and 71 days during which deer were fed only salal resulting in losses of 8.0, 17.5, 9.5 and 22.2% of body mass, respectively. Black-tailed deer, however, may lose up to 25% of their body mass during winter (Bandy 1965; Rochelle 1980). An understory of only salal may therefore sustain deer for short, critical periods of heavy snowfall, provided that the salal is not buried or too dense to restrict movement. Gates (1968) suggested that although salal associations may have high productivity, utilization may be low because of the low diversity of forage species.

Estimates of salal crude protein are varied but are generally less than 7% required for winter maintenance (Dietz 1965). Salal foliar crude protein (converted from % nitrogen·6.25 where necessary) was reported by Dealy (1959) as 4.4-6.3%, Sabhasri (1961) as 5% dry mass, Brown (1961) 5-8%, Heilman (1961) 5-7.5%, Gates (1968) 3.7-9.7%, Webber (1969) 2.3-3.8%, Dice (1970) 4.0%, Klinka (1976) 5%, a range of 5-10.8 with an average of 6.5% by Rochelle (1980), and 4.4-8.6% by McCann (1985). Stanek et al. (1979) showed that nitrogen in salal could be affected by thinning and/or fertilization. Rochelle (1980) found in vitro digestibility of salal foliage in winter at 26-33%, volatile fatty acid caloric value of 2.0 $\text{kcal}\cdot\text{g}^{-1}$, and rate of digestion was 88% over 24 hours, and 100% over 36 hours. Seip (1979) reported that in October, gross energy of current annual growth foliage was 4.8 $\text{kcal}\cdot\text{g}^{-1}$ with in vitro digestibility of 32.6% yielding 1.6 $\text{kcal}\cdot\text{g}^{-1}$ digestible energy.

Using an average live biomass (W) of 46 kg (Hovey 1984) for a Vancouver Island black-tailed deer and dry mass daily forage intake of 50 $\text{g}\cdot W^{0.75}$ (Hanley 1984), an average deer could eat about 900 g of forage per day in winter. If a conservative (high) activity increment of 2 (Hanley 1984) is used, an average deer would require $2\cdot 70W^{0.75}$ or 2473 $\text{kcal}\cdot\text{day}^{-1}$ of energy. A deer eating only salal may acquire about 1346 kcal $\cdot$ day^{-1} of metabolizable energy (900 g $\cdot$ 2.0 $\text{kcal}\cdot\text{g}^{-1}$ $\cdot$ 0.85 metabolizable energy coefficient · 0.88 digested in 24 hours) resulting in an energy deficit of around 1127 kcal$\cdot$day^{-1}. The energy deficit translates to about a 188 g$\cdot$day^{-1} biomass loss (assuming 6 kcal$\cdot$g^{-1} fat of metabolizable energy; Mautz 1978). As biomass loss occurred, energy requirements would decline, but intake rate may also decline. On a salal-only diet it would take 61 days for the average deer to reach a 25% biomass loss. Salal, however, may be only 20-50% by volume of the winter diet of black-tailed deer (Brown 1961; Gates 1968; Jones 1975; Rochelle 1980). Mixed diets are higher in digestible energy (Rochelle 1980).

An optimum tradeoff between snow interception and forage production is desired. During winter, snow buries forage reducing availability. Tall, erect shrubs are less readily buried. Because burial rates are not believed to be a linear function of snow depth, shoots taller than the depth of snow can be buried (e.g., Harestad 1979). Tallest salal shoots are in the 65-80% MCC range (Fig. 2.7) and the greatest percentage of tall shoots are also in this range (Appendix 14). Shoots under higher canopies, though, may have weaker stems (Appendix 13) and may be more readily buried by snow passing through the canopy.

Salal may be managed by using the SDI concept presented in the previous section. Lower SDI's than what would be required for salal control would be necessary. Because MCC predicted biomass well, indicated no difference among equations developed in individual variants, and has been a concept used for snow interception (Bunnell et al. 1985; McNay 1985) and forage abundance, MCC will be used in the examples that follow.

From the regressions in Chapter 2, an estimated 75 kg$\cdot$ha^{-1} of CAGBIOM and 287 kg$\cdot$ha^{-1} of FOLBIOM could be found under 80% MCC and 181 kg$\cdot$ha^{-1} CAGBIOM and 537 kg$\cdot$ha^{-1} FOLBIOM under 65% MCC. Because the abundance of arboreal lichens is low in young stands (Bunnell and Jones 1984), salal could become a more important component of winter diets. Assuming that salal was 70% of the day matter forage intake in immature stands (560 g$\cdot$day^{-1}), salal was 100% available, and deer could find all salal, CAGBIOM could support 2.23 deer$\cdot$ha^{-1} over a 60 day period in an 80% MCC stand and 5.39 deer$\cdot$ha^{-1} in a 65% MCC stand.

Under a 65% MCC canopy shoots may be shorter and more likely buried because of reduced snow interception and thus reduced forage availability. Shoots under denser canopies, however, might have weaker stems which would be displaced and buried more readily than shoots having stout stems under more open canopies. Harestad (1979) believed that 75% of forage provided by shrubs would be buried by snow depths between 50-110 cm. His estimate did not account for displacement of stems and was based upon tall, erect *Vaccinium* spp. shoots. If snow reduced salal abundance to only 1% availability (assume increased snow interception by higher canopies was offset by weaker stems being more readily buried), and deer still could find all salal, only 0.02 and 0.05 deer$\cdot$ha^{-1} could be supported by CAGBIOM over a 60 day period in stands of 80% and 65% MCC, respectively. Under severe conditions, FOLBIOM would also be consumed, potentially supporting 0.11 and 0.21 deer$\cdot$ha^{-1} under 80% and 65% MCC canopies, respectively. The severe winter of 1971-72 had $\approx$60 days with > 75 cm snowpack (Jones 1975). Although the preceding example is based on many assumptions, it indicates that twice as many deer could be supported under a 65% canopy than an 80% canopy. Continued pressure on the forage resource may reduce abundance and quality in subsequent years.

Modeling efforts like the preceding example should take into account shoot height and shoot posture. Because information on shrub burial functions is lacking and Jay (1985) identified shrub burial by snow as a critical link, I suggest that further work be done on developing shrub burial functions. Shrub burial work should include tests of the burial functions among shoots of different growth forms and among different levels of MCC. Salal height peaks under moderately closed canopies but the level of MCC where the peak occurs may be affected by stand structure (e.g., sidelighting) or age. Additional work should be done to examine the consistency of location of the peak. Attention must be given to the overstory sample design because peak locations may be sensitive to MCC measurements (e.g., size of plot, complete coverage, technique used). Because salal shoots may become weaker at increasing MCC (Appendix 13; lack of other shoots for support or too rapid elongation for amount of radial stem growth), further work should be done to verify the relationship of shoot posture to MCC.

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APPENDIX 1 Forest stand characteristics of plots

Definition of forest variables

MCC - mean crown completeness of plot (average of 52 moosehorn samples and reported as a fraction)
NTREES - number of plot trees$\cdot ha^{-1} \geq 8.0$ cm
NSAPL - # plot saplings$\cdot ha^{-1} < 8.0$ cm and > 20 cm tall
BA - basal area ($m^2 \cdot ha^{-1}$) of plot trees ≥ 8.0 cm
SUMDIA - sum of DBH (mm/225 m^2) of plot trees ≥ 8.0 cm
AVGDIA - average DBH (mm) of plot trees ≥ 8.0 cm
HT - average tree height (m) of plot trees ≥ 8.0 cm
HBLC - average height to base of live crown (m) of plot trees ≥ 8.0 cm
CRNDEP - average crown depth (HT - HBLC) of plot trees ≥ 8.0cm
DF%# - percent of NTREES that are Douglas-fir
WH%# - percent of NTREES that are western hemlock
MISC%# - percent of NTREES other than Douglas-fir and western hemlock
DF%BA - percent of BA occupied by Douglas-fir
WH%BA - percent of BA occupied by western hemlock
MISC%BA - percent of BA occupied by species other than Douglas-fir and western hemlock
AVGBADIA- DBH (mm) of tree of average basal area for trees ≥ 8.0 cm
SDI - Reineke's "stand density index" (Reineke 1933; Long 1985) computed from $NTREES \cdot (AVGBADIA/25)^{1.6}$
BAFBA - average stand basal area ($m^2 \cdot ha^{-1}$) of trees ≥ 8.0 cm determined from 5 BAF_4 prism samples
BAFDIA - average DBH (in mm) of trees ≥ 8.0 cm sampled by 5 BAF_4 prism samples
BAFTREES- average number of trees$\cdot ha^{-1} \geq 8.0$ cm determined from 5 BAF_4 prism samples
BAFSAPL - average number of saplings$\cdot ha^{-1} < 8.0$ cm determined from 5 BAF_4 prism samples
BAFBADIA- DBH (mm) of tree of average basal area determined from prism sampling
BAFSDI - Reineke's "stand density index" determined from prism sampling computed from $BAFTREES \cdot (BAFBADIA/25)^{1.6}$
DOWN - average basal area of two downslope corner prism samples
UP - average basal area of two upslope corner prism samples
RIGHT - average basal area of two right corner prism samples
LEFT - average basal area of two left corner prism samples
CENTER - basal area of prism sample in plot center

APPENDIX 1 Forest stand characteristics of plots

Plot	MCC	NTREES (#/ha)	NSAPL (#/ha)	BA (m^2/ha)	SUMDIA (mm/225m^2)	AVGDIA (mm)	HT (m)	HBLC (m)	CRNDEP (m)	DF%#	WH%#	MISC%#	DF%BA	WH%BA	MISC%BA
1	0.912	2533	4178	37.7	7469	131	12.4	3.0	9.4	25	75	0	28	72	0
2	0.782	1600	1378	46.7	6212	173	13.6	3.5	10.1	28	36	36	61	23	16
3	0.554	533	400	21.2	2559	213	13.6	2.0	11.6	50	17	33	68	14	18
4	0.793	1778	1911	53.4	7112	178	16.1	8.6	7.5	82	18	0	86	14	0
5	0.636	756	44	35.0	3991	235	25.2	17.9	7.3	100	0	0	100	0	0
6	0.783	1733	1022	34.4	5660	145	15.6	9.8	5.8	100	0	0	100	0	0
7	0.345	267	844	14.8	1316	219	15.7	2.6	13.1	33	67	0	8	92	0
8	0.651	667	800	30.7	3333	222	18.1	5.0	13.1	13	60	27	10	47	43
9	0.899	2711	3467	54.9	9096	149	15.0	7.1	7.9	16	82	2	37	62	1
10	0.746	1200	711	32.5	4461	165	15.5	5.1	10.4	96	4	0	99	1	0
11	0.895	1244	622	61.0	5877	210	15.6	6.3	9.3	0	79	21	0	62	38
12	0.641	844	1822	25.5	3401	179	12.8	4.0	8.8	68	16	16	91	4	5
13	0.799	2000	1067	62.2	8347	185	17.6	9.3	8.3	62	25	13	78	12	10
14	0.843	2444	3111	67.6	9427	171	17.4	9.9	7.4	67	22	11	84	11	5
15	0.792	2089	3289	62.0	8534	182	13.9	5.9	7.9	72	7	21	90	2	8
21	0.576	889	2133	10.1	2194	110	9.7	0.8	8.9	95	5	0	97	3	0.
22	0.416	756	400	8.5	2001	118	10.3	0.5	9.8	100	0	0	100	0	0.
23	0.809	2222	5556	41.6	7206	144	13.4	2.1	11.3	48	38	14	74	20	6
24	0.636	1111	3200	26.1	3972	159	14.3	1.5	12.8	56	20	24	64	11	25
25	0.736	1200	4311	20.0	3719	138	13.6	2.1	11.5	41	33	26	57	22	21
26	0.902	2622	7111	38.9	7576	128	12.7	3.4	9.3	8	85	7	28	62	10
27	0.757	1378	8000	17.5	3676	119	11.5	2.8	8.7	61	32	7	52	30	18

APPENDIX 1 continued

Plot	AVGBADIA (mm)	SDI	BAFBA (m^2/ha)	BAFDIA (mm)	BAFTREES (#/ha)	BAFSAPL (#/ha)	BAFBADIA (mm)	BAFSDI	DOWN (m^2/ha)	UP (m^2/ha)	RIGHT (m^2/ha)	LEFT (m^2/ha)	CENTER (m^2/ha)
1	138	974	30.4	168	2018	365	138	784	3	26	28	28	40
2	193	1055	40.0	249	1312	1065	197	896	44	36	36	44	40
3	225	450	30.4	256	927	0	204	671	34	34	42	26	16
4	196	1201	48.0	230	1637	1121	193	1084	52	44	50	46	48
5	243	722	36.8	385	462	0	318	681	36	28	28	36	56
6	159	839	31.2	229	1155	1087	185	716	36	32	36	32	20
7	266	295	18.4	255	730	0	179	428	22	20	20	22	8
8	242	634	32.8	288	638	0	256	662	32	36	30	38	28
9	161	1335	58.4	182	3325	2661	150	1461	54	72	54	70	40
10	186	746	38.4	268	1239	404	199	858	44	36	38	42	32
11	250	1243	59.2	440	1062	731	266	1176	48	72	66	54	56
12	196	572	28.8	234	909	208	201	640	30	30	36	24	24
13	199	1388	53.6	241	1711	0	200	1195	52	48	50	50	68
14	188	1544	59.2	222	2546	1033	172	1400	48	60	54	54	80
15	194	1397	41.6	253	1361	648	197	932	36	32	44	34	52
21	120	275	12.0	141	1095	5091	118	330	14	14	16	12	4
22	120	233	8.8	144	741	564	123	238	12	8	4	16	4
23	154	1028	31.2	190	1625	5954	156	767	32	28	36	26	36
24	173	616	25.6	214	1027	393	178	597	24	26	28	22	28
25	146	505	24.0	203	1390	5012	148	603	24	22	18	28	40
26	137	1005	31.2	173	2250	5170	133	818	30	24	28	26	48
27	127	467	21.6	181	1481	2064	136	561	26	18	22	22	24

APPENDIX 2 Means and 95% confidence intervals for understory characteristics of plots

Definition of understory variables

DENSITY - backtransformed average density of shoots$\cdot m^{-2}$
CAGBIOM - backtransformed average current annual growth foliar biomass ($g \cdot m^{-2}$) per plot
FOLBIOM - backtransformed average estimated standing crop foliar biomass ($g \cdot m^{-2}$) per plot (excludes CAGBIOM)
TOTBIOM - backtransformed average estimated standing crop foliar and woody stem biomass ($g \cdot m^{-2}$) per plot (excludes CAGBIOM)
PCTCOVER- backtransformed average quadrat (0.25 m^2) percent cover of salal per plot
REPHT - backtransformed average repose height (cm) per shoot per plot
STRHT - backtransformed average stretch height (cm) per shoot per plot
BASDIA - backtransformed average basal diameter (cm) per shoot per plot

APPENDIX 2 Means and 95% confidence intervals for understory characteristics of plots

Plot	DENSITY (#·m^{-2})[a]		CAGBIOM (g·m^{-2})[a]		FOLBIOM (g·m^{-2})[a]		TOTBIOM (g·m^{-2})[a]	
	$\bar{x}$	0.95 C.I.	$\bar{x}$	0.95 C.I.	$\bar{x}$	0.95 C.I.	$\bar{x}$	0.95 C.I.
1	0.65	0.11- 1.65	0.02	0.00- 0.08	0.08	0.01- 0.32	0.23	0.02- 0.95
2	10.83	6.86- 15.70	2.13	1.00- 3.88	5.57	2.96- 9.40	20.07	10.05- 35.20
3	40.58	31.06- 51.37	11.31	7.91-15.57	22.54	15.47- 31.48	106.27	70.50-152.45
4	14.41	10.33- 19.16	6.65	4.11-10.06	20.04	11.48- 32.05	66.27	35.56-110.96
5	28.16	23.55- 33.18	28.13	20.02-38.17	72.50	52.74- 96.66	271.07	189.42-373.34
6	16.47	12.81- 20.60	25.56	15.15-39.88	93.86	58.73-140.76	400.28	242.96-614.03
7	67.99	57.16- 79.75	64.65	50.40-81.37	172.62	130.86-222.43	633.57	466.92-835.80
8	13.84	8.79- 20.04	6.14	2.95-11.05	14.49	7.27- 25.39	46.81	22.33- 84.72
9	0.12	0.01- 0.38	0.00	0.00- 0.01	0.01	0.00- 0.07	0.06	0.00- 0.31
10	15.65	12.37- 19.31	13.50	8.73-19.74	29.44	17.49- 45.87	133.79	80.88-205.83
11	1.03	0.34- 2.09	0.01	0.00- 0.03	0.20	0.04- 0.57	0.63	0.11- 1.86
12	20.89	16.76- 25.48	26.09	17.68-36.81	53.62	30.83- 85.54	240.84	121.15-421.07
13	14.50	11.13- 18.31	5.58	3.42- 8.48	16.07	7.99- 28.31	73.33	37.59-126.61
14	1.57	0.63- 2.93	0.18	0.05- 0.44	0.29	0.05- 0.89	1.39	0.24- 4.21
15	12.12	9.14- 15.52	14.61	8.70-22.73	30.64	15.35- 53.71	135.47	58.62-260.58
21	102.07	85.54-120.06	36.48	30.90-42.70	119.57	90.82-153.83	278.07	211.97-356.66
22	144.47	124.92-165.45	55.59	45.87-66.58	119.79	88.64-157.51	289.17	216.74-376.14
23	12.68	8.59- 17.56	3.33	1.82- 5.49	40.01	19.78- 70.74	92.61	46.36-162.43
24	50.44	37.89- 64.77	19.38	13.68-26.49	72.05	46.22-106.06	165.15	105.64-243.63
25	24.51	16.83- 33.63	7.98	4.53-12.86	62.67	35.45-101.12	143.59	81.24-231.68
26	5.66	2.93- 9.29	0.58	0.22- 1.22	3.05	1.09- 6.54	7.22	2.63- 15.34
27	39.96	29.17- 52.45	13.99	8.89-20.76	97.98	60.29-148.81	226.96	139.36-345.19

[a] Backtransformed average of 52 0.25m^2 quadrats x 4.

APPENDIX 2 continued

Plot	PCTCOVER (%)			REPHT ($\mathrm{cm \cdot shoot^{-1}}$)			STRHT ($\mathrm{cm \cdot shoot^{-1}}$)			BASDIA ($\mathrm{cm \cdot shoot^{-1}}$)		
	n	$\bar{x}$	0.95 C.I.	n	$\bar{x}$	0.95 C.I.	n	$\bar{x}$	0.95 C.I.	n	$\bar{x}$	0.95 C.I.
1	52	0.38	0.05- 1.01	44	15.40	12.36-18.77	44	25.26	18.93-32.49	44	0.21	0.18-0.24
2	52	9.57	6.23-13.64	208	15.50	13.68-17.43	209	23.79	21.14-26.60	209	0.26	0.24-0.28
3	52	17.73	13.12-23.03	567	17.93	16.67-19.25	569	24.20	22.39-26.08	570	0.30	0.29-0.32
4	52	17.88	13.36-23.06	225	20.69	18.60-22.88	227	32.22	28.81-35.81	227	0.29	0.27-0.32
5	52	51.13	43.84-58.98	350	30.21	27.89-32.63	354	47.22	43.46-51.13	354	0.39	0.37-0.41
6	52	38.47	32.78-44.61	237	50.09	45.50-54.91	237	74.85	67.52-82.56	237	0.54	0.49-0.59
7	52	50.33	43.54-57.61	878	35.04	33.25-36.88	881	43.08	40.87-45.35	881	0.41	0.39-0.42
8	52	14.83	9.39-21.50	269	19.06	17.08-21.15	269	27.30	24.23-30.56	269	0.28	0.26-0.30
9	52	0.06	0.00- 0.24	12	17.21	12.06-23.28	12	34.76	24.04-47.46	12	0.34	0.26-0.44
10	52	40.13	32.45-48.63	221	31.23	28.57-34.01	221	59.06	53.76-64.60	221	0.47	0.44-0.50
11	52	0.95	0.36- 1.81	43	14.85	12.59-17.30	44	24.39	20.38-28.76	43	0.24	0.21-0.27
12	52	44.05	35.90-53.04	279	46.43	41.65-51.48	280	67.64	60.27-75.43	280	0.45	0.41-0.49
13	52	26.38	20.21-33.36	217	30.07	26.72-33.61	217	39.98	35.23-45.04	217	0.33	0.31-0.36
14	52	0.85	0.36- 1.54	53	19.31	14.88-24.32	53	26.88	20.22-34.49	53	0.25	0.20-0.30
15	52	28.98	23.68-34.82	185	52.61	46.53-59.06	186	76.75	67.25-86.87	186	0.49	0.44-0.54
21	52	52.87	45.72-60.54	1295	19.70	18.95-20.47	1296	27.23	26.14-28.33	1294	0.30	0.29-0.30
22	52	48.66	40.42-57.65	1751	15.96	15.43-16.50	1751	22.60	21.79-23.43	1750	0.31	0.31-0.32
23	52	12.22	7.71-17.77	209	27.74	24.40-31.31	209	43.35	37.96-49.09	209	0.37	0.35-0.40
24	52	33.55	25.81-42.30	682	22.42	21.29-23.59	682	32.30	30.53-34.11	680	0.30	0.29-0.31
25	52	23.05	17.09-29.90	399	28.02	25.99-30.12	399	39.06	36.11-42.12	399	0.35	0.34-0.37
26	52	2.63	1.26- 4.50	126	16.98	14.65-19.49	126	24.28	20.83-28.00	126	0.27	0.25-0.30
27	52	26.62	20.63-33.37	608	28.25	26.77-29.77	608	43.87	41.62-46.18	608	0.34	0.33-0.35

APPENDIX 3 Correlation coefficients among overstory variables for CWHa (*n*=10)

	MCC	NTREES	NSAPL	BA	SUMDIA	AVGDIA	HT	HBLC	CRNDEP	DF%#	WH%#	MISC%#
MCC	1.00											
NTREES	.92	1.00										
NSAPL	.69	.87	1.00									
BA	.83	.79	.55	1.00								
SUMDIA	.93	.97	.79	.91	1.00							
AVGDIA	-.81	-.88	-.75	-.53	-.79	1.00						
HT	-.26	-.40	-.52	-.06	-.28	.63	1.00					
HBLC	.13	.01	-.27	.28	.13	.21	.86	1.00				
CRNDEP	-.62	-.60	-.24	-.62	-.65	.49	-.22	-.69	1.00			
DF%#	-.01	-.16	-.48	-.02	-.11	.03	.45	.63	-.58	1.00		
WH%#	.08	.32	.68	.09	.24	-.18	-.39	-.50	.41	-.90	1.00	
MISC%#	-.16	-.31	-.28	-.12	-.25	.32	-.24	-.44	.50	-.45	.03	1.00
DF%BA	.24	.04	-.38	.23	.13	-.12	.31	.58	-.68	.91	-.92	-.21
WH%BA	-.18	.11	.53	-.17	-.01	-.05	-.34	-.51	.49	-.79	.93	-.11
MISC%BA	-.18	-.38	-.28	-.19	-.33	.43	.01	-.31	.60	-.50	.18	.79
AVGBADIA	-.90	-.92	-.74	-.60	-.84	.97	.52	.08	.59	-.03	-.10	.26
SDI	.89	.89	.67	.98	.97	-.66	-.17	.21	-.64	-.06	.15	-.18
BAFBA	.69	.64	.40	.90	.78	-.36	-.03	.29	-.51	-.01	.05	-.09
BAFDIA	-.51	-.72	-.83	-.34	-.60	.81	.87	.60	.09	.45	-.55	.11
BAFTREES	.71	.88	.85	.70	.86	-.73	-.47	-.16	-.37	-.35	.51	-.26
BAFSAPL	.65	.78	.57	.79	.82	-.62	-.28	.08	-.54	-.16	.26	-.19
BAFBADIA	-.36	-.62	-.73	-.20	-.47	.77	.89	.65	-.02	.38	-.51	.17
BAFSDI	.74	.77	.59	.88	.86	-.54	-.20	.11	-.48	-.13	.22	-.14
DOWN	.65	.58	.28	.87	.73	-.40	-.06	.23	-.53	.16	-.15	-.06
UP	.55	.59	.43	.72	.68	-.35	-.14	.07	-.32	-.23	.27	.02
RIGHT	.55	.53	.30	.71	.64	-.39	-.25	.04	-.44	.06	-.09	.04
LEFT	.61	.60	.39	.83	.72	-.34	-.01	.21	-.38	-.15	.21	-.08
CENTER	.61	.46	.28	.75	.61	-.13	.43	.61	-.55	.20	.13	-.20

	DF%BA	WH%BA	MISC%BA	AVGBADIA	SDI	BAFBA	BAFDIA	BAFTREES	BAFSAPL	BAFBADIA	BAFSDI	DOWN
WH%BA	-.92	1.00										
MISC%BA	-.42	.04	1.00									
AVGBADIA	-.22	.08	.38	1.00								
SDI	.19	-.10	-.26	-.72	1.00							
BAFBA	.26	-.23	-.14	-.45	.87	1.00						
BAFDIA	.34	-.47	.21	.72	-.47	-.22	1.00					
BAFTREES	-.15	.31	-.34	-.72	.78	.72	-.76	1.00				
BAFSAPL	.07	.06	-.30	-.61	.83	.82	-.56	.87	1.00			
BAFBADIA	.31	-.49	.34	.64	-.34	-.11	.96	-.70	-.50	1.00		
BAFSDI	.13	-.05	-.22	-.59	.90	.96	-.47	.88	.90	-.37	1.00	
DOWN	.43	-.39	-.19	-.46	.83	.95	-.22	.63	.78	-.14	.91	1.00
UP	.01	.01	-.02	-.40	.72	.91	-.38	.80	.87	-.28	.93	.83
RIGHT	.33	-.32	-.11	-.46	.70	.86	-.39	.67	.76	-.30	.87	.90
LEFT	.08	-.06	-.07	-.40	.80	.95	-.24	.74	.86	-.15	.94	.88
CENTER	.36	-.31	-.20	-.28	.69	.65	.20	.27	.28	.31	.52	.58

	UP	RIGHT	LEFT	CENTER
UP	1.00			
RIGHT	.86	1.00		
LEFT	.94	.76	1.00	
CENTER	.32	.30	.52	1.00

APPENDIX 4 Correlation coefficients among overstory variables for CWHb: ($n=5$)

	MCC	NTREES	NSAPL	BA	SUMDIA	AVGDIA	HT	HBLC	CRNDEP	DF%#	WH%#	MISC%#
MCC	1.00											
NTREES	.49	1.00										
NSAPL	-.14	.58	1.00									
BA	.89	.82	.16	1.00								
SUMDIA	.60	.99	.48	.89	1.00							
AVGDIA	.49	-.46	-.75	.13	-.31	1.00						
HT	.66	.66	-.16	.75	.70	-.02	1.00					
HBLC	.58	.82	.10	.77	.82	-.25	.97	1.00				
CRNDEP	-.07	-.88	-.84	-.45	-.79	.82	-.37	-.60	1.00			
DF%#	-.60	.40	.71	-.19	.27	-.94	-.12	.11	-.73	1.00		
WH%#	.62	-.36	-.73	.21	-.24	.89	.22	-.01	.69	-.99	1.00	
MISC%#	.13	-.42	-.15	-.07	-.32	.67	-.60	-.68	.55	-.49	.36	1.00
DF%BA	-.65	.34	.68	-.25	.21	-.94	-.16	.06	-.69	.99	-.99	-.48
WH%BA	.66	-.33	-.68	.26	-.20	.91	.20	-.02	.67	-.99	.99	.42
MISC%BA	.63	-.36	-.68	.24	-.22	.97	.09	-.13	.72	-.99	.96	.58
AVGBADIA	.52	-.48	-.73	.11	-.34	.98	.01	-.23	.80	-.99	.96	.60
SDI	.81	.90	.28	.99	.95	-.03	.75	.81	-.58	-.03	.06	-.16
BAFBA	.93	.54	-.21	.86	.63	.33	.87	.79	-.15	-.50	.57	-.21
BAFDIA	.58	-.41	-.63	.18	-.28	.96	-.01	-.22	.74	-.98	.94	.65
BAFTREES	.40	.87	.48	.64	.81	-.57	.76	.89	-.84	.36	-.26	-.74
BAFSAPL	.58	.41	.50	.50	.40	-.02	.15	.23	-.37	-.22	.22	.09
BAFBADIA	.39	-.58	-.75	-.01	-.45	.99	-.15	-.38	.88	-.94	.89	.69
BAFSDI	.85	.72	.01	.88	.76	.06	.93	.91	-.40	-.25	.34	-.41
DOWN	.79	.51	-.37	.77	.60	.28	.95	.85	-.11	-.39	.47	-.36
UP	.85	.15	-.43	.58	.24	.55	.65	.50	.20	-.77	.83	-.06
RIGHT	.93	.18	-.43	.68	.30	.68	.60	.44	.23	-.82	.85	.15
LEFT	.90	.51	-.27	.81	.59	.33	.90	.80	-.12	-.50	.58	-.27
CENTER	.77	.86	.16	.91	.89	-.11	.92	.95	-.58	-.04	.12	-.46

	DF%BA	WH%BA	MISC%BA	AVGBADIA	SDI	BAFBA	BAFDIA	BAFTREES	BAFSAPL	BAFBADIA	BAFSDI	DOWN
WH%BA	-.99	1.00										
MISC%BA	-.99	.98	1.00									
AVGBADIA	-.98	.97	.99	1.00								
SDI	-.10	.10	.08	-.04	1.00							
BAFBA	-.55	.58	.49	.39	.80	1.00						
BAFDIA	-.98	.97	.99	.99	.03	.41	1.00					
BAFTREES	.32	-.27	-.40	-.49	.72	.59	-.45	1.00				
BAFSAPL	-.24	.27	.20	.12	.48	.47	.23	.46	1.00			
BAFBADIA	-.92	.90	.96	.98	-.17	.22	.96	-.65	.02	1.00		
BAFSDI	-.30	.34	.23	.12	.86	.96	.15	.79	.50	-.05	1.00	
DOWN	-.43	.46	.38	.29	.73	.92	.28	.56	.14	.16	.91	1.00
UP	-.79	.83	.72	.66	.48	.90	.67	.32	.49	.50	.78	.78
RIGHT	-.85	.87	.81	.74	.56	.90	.76	.21	.48	.61	.75	.77
LEFT	-.54	.58	.48	.39	.76	.99	.40	.58	.40	.22	.96	.96
CENTER	-.10	.13	.04	-.08	.93	.89	-.04	.86	.45	-.23	.97	.86

	UP	RIGHT	LEFT	CENTER
UP	1.00			
RIGHT	.96	1.00		
LEFT	.90	.89	1.00	
CENTER	.61	.60	.87	1.00

APPENDIX 5 Correlation coefficients among overstory variables for CWHb, (n=7)

	MCC	NTREES	NSAPL	BA	SUMDIA	AVGDIA	HT	HBLC	CRNDEP	DF%#	WH%#	MISC%#
MCC	1.00											
NTREES	.88	1.00										
NSAPL	.90	.73	1.00									
BA	.82	.92	.60	1.00								
SUMDIA	.86	.98	.67	.98	1.00							
AVGDIA	.29	.24	.10	.58	.42	1.00						
HT	.56	.44	.38	.70	.59	.93	1.00					
HBLC	.94	.81	.95	.68	.76	.18	.48	1.00				
CRNDEP	.01	-.05	-.21	.34	.15	.94	.81	-.13	1.00			
DF%#	-.91	-.84	-.74	-.82	-.85	-.46	-.72	-.89	-.21	1.00		
WH%#	.90	.91	.77	.79	.87	.20	.47	.92	-.08	-.94	1.00	
MISC%#	.34	.08	.17	.37	.24	.86	.91	.25	.86	-.49	.18	1.00
DF%BA	-.86	-.70	-.84	-.63	-.68	-.31	-.59	-.95	-.03	.93	-.90	-.40
WH%BA	.87	.85	.82	.66	.77	.06	.36	.94	-.23	-.89	.98	.08
MISC%BA	.37	.02	.41	.21	.12	.66	.76	.44	.56	-.49	.24	.83
AVGBADIA	.34	.26	.15	.61	.44	.99	.92	.21	.90	-.48	.22	.85
SDI	.84	.94	.63	.99	.99	.53	.66	.71	.27	-.83	.82	.32
BAFBA	.90	.84	.74	.94	.91	.66	.83	.80	.40	-.91	.81	.58
BAFDIA	.49	.25	.41	.52	.39	.89	.95	.44	.78	-.60	.32	.94
BAFTREES	.94	.93	.83	.77	.87	.08	.36	.92	-.21	-.88	.97	.08
BAFSAPL	.61	.58	.36	.47	.54	-.11	.08	.38	-.16	-.43	.48	.02
BAFBADIA	.28	.16	.17	.51	.34	.97	.90	.18	.90	-.40	.12	.86
BAFSDI	.94	.89	.78	.94	.93	.56	.76	.85	.29	-.94	.87	.50
DOWN	.93	.85	.84	.91	.90	.55	.74	.85	.27	-.87	.79	.48
UP	.78	.67	.58	.87	.79	.79	.88	.61	.59	-.78	.61	.71
RIGHT	.80	.75	.66	.89	.83	.62	.70	.63	.37	-.69	.61	.46
LEFT	.78	.66	.65	.74	.72	.62	.84	.75	.45	-.87	.71	.71
CENTER	.89	.79	.71	.83	.83	.56	.81	.85	.34	-.98	.87	.61

	DF%BA	WH%BA	MISC%BA	AVGBADIA	SDI	BAFBA	BAFDIA	BAFTREES	BAFSAPL	BAFBADIA	BAFSDI	DOWN
WH%BA	-.92	1.00										
MISC%BA	-.61	.26	1.00									
AVGBADIA	-.34	.09	.67	1.00								
SDI	-.65	.70	.18	.55	1.00							
BAFBA	-.79	.72	.50	.69	.93	1.00						
BAFDIA	-.56	.25	.89	.89	.48	.73	1.00					
BAFTREES	-.83	.95	.13	.12	.81	.79	.23	1.00				
BAFSAPL	-.22	.40	-.26	-.06	.50	.43	-.04	.64	1.00			
BAFBADIA	-.31	.01	.74	.98	.45	.62	.92	.02	-.19	1.00		
BAFSDI	-.82	.79	.45	.60	.94	.99	.65	.86	.48	.52	1.00	
DOWN	-.78	.73	.46	.58	.91	.97	.68	.80	.43	.55	.97	1.00
UP	-.63	.49	.57	.84	.85	.95	.81	.60	.39	.78	.91	.89
RIGHT	-.56	.50	.37	.69	.88	.91	.63	.65	.43	.64	.89	.90
LEFT	-.77	.65	.60	.58	.73	.87	.78	.65	.33	.57	.86	.86
CENTER	-.88	.80	.55	.57	.83	.93	.70	.82	.45	.50	.95	.89

	UP	RIGHT	LEFT	CENTER
UP	1.00			
RIGHT	.94	1.00		
LEFT	.77	.62	1.00	
CENTER	.83	.71	.94	1.00

APPENDIX 8 Correlation coefficients among overstory variables for all three variants (*n*=22)

	MCC	NTREES	NSAPL	BA	SUMDIA	AVGDIA	HT	HBLC	CRNDEP	DF%#	WH%#	MISC%#
MCC	1.00											
NTREES	.85	1.00										
NSAPL	.46	.56	1.00									
BA	.74	.69	.01	1.00								
SUMDIA	.85	.93	.33	.90	1.00							
AVGDIA	-.21	-.41	-.61	.27	-.10	1.00						
HT	.07	-.08	-.42	.40	.17	.74	1.00					
HBLC	.28	.17	-.32	.54	.38	.49	.88	1.00				
CRNDEP	-.47	-.48	-.03	-.46	-.52	.19	-.18	-.63	1.00			
DF%#	-.35	-.25	-.29	-.25	-.24	-.16	.08	.27	-.43	1.00		
WH%#	.37	.34	.35	.22	.27	.04	-.07	-.19	.28	-.93	1.00	
MISC%#	.05	-.16	-.05	.13	-.03	.32	-.05	-.26	.46	-.44	.07	1.00
DF%BA	-.15	-.04	-.20	-.06	-.01	-.22	.02	.25	-.48	.92	-.92	-.23
WH%BA	.13	.16	.24	.05	.08	.11	-.05	-.21	.34	-.82	.94	-.07
MISC%BA	.10	-.24	.01	.06	-.14	.32	.06	-.20	.49	-.58	.33	.74
AVGBADIA	-.22	-.42	-.61	.26	-.12	.98	.68	.42	.23	-.22	.12	.29
SDI	.80	.79	.12	.99	.96	.14	.31	.49	-.49	-.25	.24	.08
BAFBA	.68	.54	-.11	.93	.78	.39	.49	.59	-.41	-.28	.26	.13
BAFDIA	.06	-.32	-.52	.35	-.04	.82	.70	.56	-.01	-.15	.05	.26
BAFTREES	.70	.88	.53	.55	.79	-.41	-.14	.07	-.36	-.33	.45	-.19
BAFSAPL	.27	.35	.64	-.13	.13	-.61	-.41	-.34	.02	-.15	.19	-.07
BAFBADIA	-.02	-.35	-.59	.31	-.05	.88	.82	.67	-.03	-.01	-.09	.26
BAFSDI	.75	.68	.04	.92	.86	.21	.36	.50	-.43	-.31	.32	.07
DOWN	.64	.50	-.16	.86	.72	.38	.49	.60	-.42	-.19	.17	.08
UP	.58	.42	-.18	.80	.63	.37	.39	.45	-.30	-.38	.36	.15
RIGHT	.62	.44	-.15	.86	.68	.42	.36	.46	-.36	-.27	.22	.21
LEFT	.59	.47	-.18	.82	.68	.34	.49	.56	-.36	-.30	.30	.06
CENTER	.70	.60	.13	.87	.79	.26	.54	.62	-.41	-.20	.17	.13

	DF%BA	WH%BA	MISC%BA	AVGBADIA	SDI	BAFBA	BAFDIA	BAFTREES	BAFSAPL	BAFBADIA	BAFSDI	DOWN
WH%BA	-.93	1.00										
MISC%BA	-.56	.21	1.00									
AVGBADIA	-.31	.21	.33	1.00								
SDI	-.05	.06	-.01	.13	1.00							
BAFBA	-.13	.09	.13	.39	.90	1.00						
BAFDIA	-.22	.06	.42	.83	.22	.47	1.00					
BAFTREES	-.15	.29	-.25	-.40	.65	.54	-.41	1.00				
BAFSAPL	-.01	.05	-.08	-.60	-.03	-.21	-.47	.36	1.00			
BAFBADIA	-.06	-.10	.36	.83	.18	.42	.93	-.46	-.55	1.00		
BAFSDI	-.13	.14	.04	.22	.92	.97	.27	.71	.09	.21	1.00	
DOWN	-.04	.04	.03	.38	.83	.95	.43	.49	-.25	.41	.93	1.00
UP	-.26	.20	.22	.40	.76	.94	.47	.52	-.20	.37	.92	.88
RIGHT	-.12	.07	.17	.43	.82	.94	.50	.43	-.22	.41	.90	.90
LEFT	-.18	.16	.10	.35	.79	.94	.40	.56	-.21	.37	.93	.93
CENTER	-.03	.01	.10	.22	.86	.83	.37	.48	-.06	.35	.81	.73

	UP	RIGHT	LEFT	CENTER
UP	1.00			
RIGHT	.93	1.00		
LEFT	.93	.83	1.00	
CENTER	.64	.67	.69	1.00

APPENDIX 7

Allometric equations for standing crop foliar and total biomass of salal

Allometric relationships were determined from a random sample of shoots selected to be representative of the range of shoot sizes. Current annual growth leaves and twigs were removed and discarded. All living older leaves were separated from stem material, dried at 65°C for 24 hours and weighed to the nearest 0.01 g. Stem material was cut into small pieces for quicker drying and dried at 65°C for 48 hours and weighed. Equations relating foliar biomass and stem+foliar biomass (total standing crop biomass) were developed with basal diameter, stretch height, and various combinations of these two used as independent variables.

Slope and equation tests among all equations developed for individual plots were performed on ln-ln transformed equations. Separate tests were made with ln(BASDIA) and $\ln(\mathrm{BASDIA}^2 \cdot \mathrm{STRHT})$ as independent variables. Significant differences ($p < 0.05$) were found among equations in all cases except for equations developed in plots 21, 22 and 24 which were sampled in the same stand.

Allometric equations were developed for each plot using ln transformed variables, untransformed variables, and for a nonlinear function. Indices of determination (i^2, Ezekiel and Fox 1970) and $s_{y.x}$'s were computed for ln transformed equations. A combination of forward and backward stepwise regression was used to identify the best simple or multiple linear regression for each data set. Derivative-free nonlinear regressions of the form $a \cdot (\mathrm{BASDIA}^2 \cdot \mathrm{STRHT})^b$ were computed with a FORTRAN subroutine (Moore 1984).

From the sets of equations developed for each plot the equation having the lowest $s_{y.x}$ was selected to be used. Log transformed equations were never better than untransformed equations, but they did meet the assumption of homogeneity of variance while untransformed and power equations were strongly heteroscedastic.

Time and logistic constraints prevented clipping of salal shoots in many plots. Equations applied to unsampled plots were based on plots either in similar geographic locations or with similar growth form of salal. Salal growth form was very different among the plots used to develop allometric equations, but all unsampled plots had shoot growth form similar to those plots sampled. The following table presents the best equations found and plots to which the equations were applied for estimates of foliar and total standing crop biomass.

Ezekiel, M. and K.A. Fox. 1970. Methods of correlation and regression analaysis. 3rd. ed. John Wiley and Sons, Inc. New York, NY.

Moore, C. 1984. UBC CURVE. Computing Centre. University of British Columbia, Vancouver, B.C.

APPENDIX 7 Salal standing crop foliar and total biomass allometric equations. Y1=FOLBIOM ($g \cdot shoot^{-1}$), Y2=TOTBIOM ($g \cdot shoot^{-1}$), X1=BASDIA, X2=STRHT, $X3=X1^2$, $X4=X2^2$, $X5=X1 \cdot X2$, $X6=X3 \cdot X2$, $X7=X1 \cdot X4$, $X8=X3 \cdot X4$

Plots sampled	Equation	*n*	R^2	$s_{y \cdot x}$
1[a]	$Y1 = 0.02539 \cdot X2$	42	0.40	0.66
1	$Y2 = 0.3957 \cdot X5 - 0.00224 \cdot X7$	42	0.76	1.36
2[b]	$Y1 = 0.2921 \cdot X5 - 0.000759 \cdot X4 - 0.4598 \cdot X6 + 0.00297 \cdot X8$	117	0.52	0.60
2	$Y2 = 7.512 \cdot X3 - 0.00489 \cdot X4 + 0.7451 \cdot X5 - 1.352 \cdot X6 + 0.01281 \cdot X7$	117	0.87	1.57
3[c]	$Y1 = 0.31695 \cdot X6^{0.60968}$	97	0.53	0.59
3	$Y2 = 1.10036 \cdot X6^{0.76637}$	97	0.88	1.35
4[d]	$Y1 = 0.39828 \cdot X6^{0.78170}$	76	0.77	1.53
4	$Y2 = 0.89957 \cdot X6^{0.91897}$	76	0.93	3.15
5[e]	$Y1 = 0.40376 \cdot X6^{0.72209}$	93	0.81	3.05
5	$Y2 = 0.99106 \cdot X6^{0.83684}$	93	0.90	9.31
10[f]	$Y1 = 0.07619 \cdot X6^{1.03167}$	32	0.95	2.11
10	$Y2 = 0.42300 \cdot X6^{0.98053}$	32	0.98	5.02
15[g]	$Y1 = 0.02246 \cdot X6^{1.15984}$	49	0.85	10.10
15	$Y2 = 0.01716 \cdot X6^{1.49132}$	49	0.85	81.31
21,22,24[h]	$Y1 = -0.000784 \cdot X4 + 0.1208 \cdot X5 - 0.1942 \cdot X6 + 0.00352 \cdot X7$	151	0.85	1.16
21,22,24	$Y2 = 0.6287 - 0.1024 \cdot X2 + 0.3971 \cdot X5 - 0.3617 \cdot X6 + 0.00510 \cdot X7$	151	0.93	1.86

[a] Equation used for plots 1, 9, and 11.

[b] Equation used for plot 2.

[c] Equation used for plot 3.

[d] Equation used for plots 4 and 8.

[e] Equation used for plots 5, 6, and 7.

[f] Equation used for plots 10, 13, and 14.

[g] Equation used for plots 12 and 15.

[h] Equation used for plots 21 - 27.

APPENDIX 8 Average biomass (in grams) of salal leaves by plot and 95% confidence intervals (backtransformed from square root)

Plot	*n*	$\bar{x}$	0.95 Confidence int.
1	330	0.0987	0.0914 - 0.1062
2	315	0.1239	0.1148 - 0.1333
3	847	0.1133	0.1082 - 0.1184
4	506	0.1432	0.1352 - 0.1513
5	646	0.2306	0.2188 - 0.2426
6	620	0.2429	0.2324 - 0.2536
7	672	0.1941	0.1839 - 0.2047
8	653	0.1294	0.1215 - 0.1375
9	162	0.0728	0.0644 - 0.0817
10	792	0.1831	0.1745 - 0.1919
11[a]			
12	865	0.2049	0.1954 - 0.2147
13	809	0.1774	0.1700 - 0.1850
14	583	0.1359	0.1286 - 0.1434
15	922	0.1839	0.1762 - 0.1918
21	1187	0.1338	0.1281 - 0.1395
22	1450	0.1204	0.1154 - 0.1256
23	1245	0.1118	0.1075 - 0.1161
24	1115	0.1303	0.1244 - 0.1363
25	1003	0.1394	0.1337 - 0.1453
26	627	0.0935	0.0887 - 0.0985
27	1094	0.1524	0.1462 - 0.1587

[a] Leaf biomass from UBCRF plot 8 was used.

APPENDIX 9 Regressions of salal variables against plot and prism basal areas and stand densities. Sample sizes: CWHa=10, $CWHb_1$=5, $CWHb_3$=7. Equations significant at $p \leq 0.05$. Regression equation: $Y = b_0 + b_1X$

Y	Variant	X	b_0	b_1	r^2	$s_{y \cdot x}$
DENSITY:	CWHa+b_1	1/NTREES [a]	N.S.[b]	17731	0.86	6.73
		1/BA	-14.094	1111.1	0.81	8.02
		1/SDI	-11.505	22351.0	0.86	6.97
		1/BAFTREES	N.S.	19106	0.31	14.76
		1/BAFBA	-23.725	1499.0	0.68	10.47
	$CWHb_3$	1/NTREES	-61.237	140890	0.88	19.57
		1/BA	-25.221	1350.8	0.92	15.71
		1/SDI	-31.878	38548.0	0.93	14.96
		1/BAFTREES	-74.65	158560	0.85	21.84
		1/BAFBA	-34.597	1602.6	0.95	12.01
CAGBIOM:	All 3	1/NTREES	N.S.	16807	0.54	12.09
		1/BA	N.S.	442.33	0.59	11.60
		1/SDI	N.S.	11170	0.70	10.67
		1/BAFTREES	N.S.	18784	0.34	14.72
		1/BAFBA	N.S.	471.21	0.56	12.27
FOLBIOM:	All 3	1/NTREES	N.S.	46956	0.42	37.24
		1/BA	N.S.	1293.1	0.59	31.17
		1/SDI	N.S.	32432	0.66	29.11
		BAFTREES	100.91	-0.03828	0.29	41.86
		BAFBA	135.61	-2.5425	0.57	32.52
TOTBIOM:	All 3	1/NTREES	N.S.	156470	0.52	108.42
		1/BA	N.S.	3785.9	0.33	128.89
		1/SDI	N.S.	97566	0.45	117.05
		BAFTREES	331.49	-0.12924	0.31	133.61
		BAFBA	385.04	-6.7463	0.38	126.56
PCTCOVER:	All 3	NTREES	49.774	-0.0170	0.47	13.66
		BA	47.809	-0.63628	0.39	14.66
		SDI	50.226	-0.3043	0.44	14.01
		BAFTREES	50.373	-0.01850	0.47	13.69
		BAFBA	51.843	-0.78680	0.38	14.75

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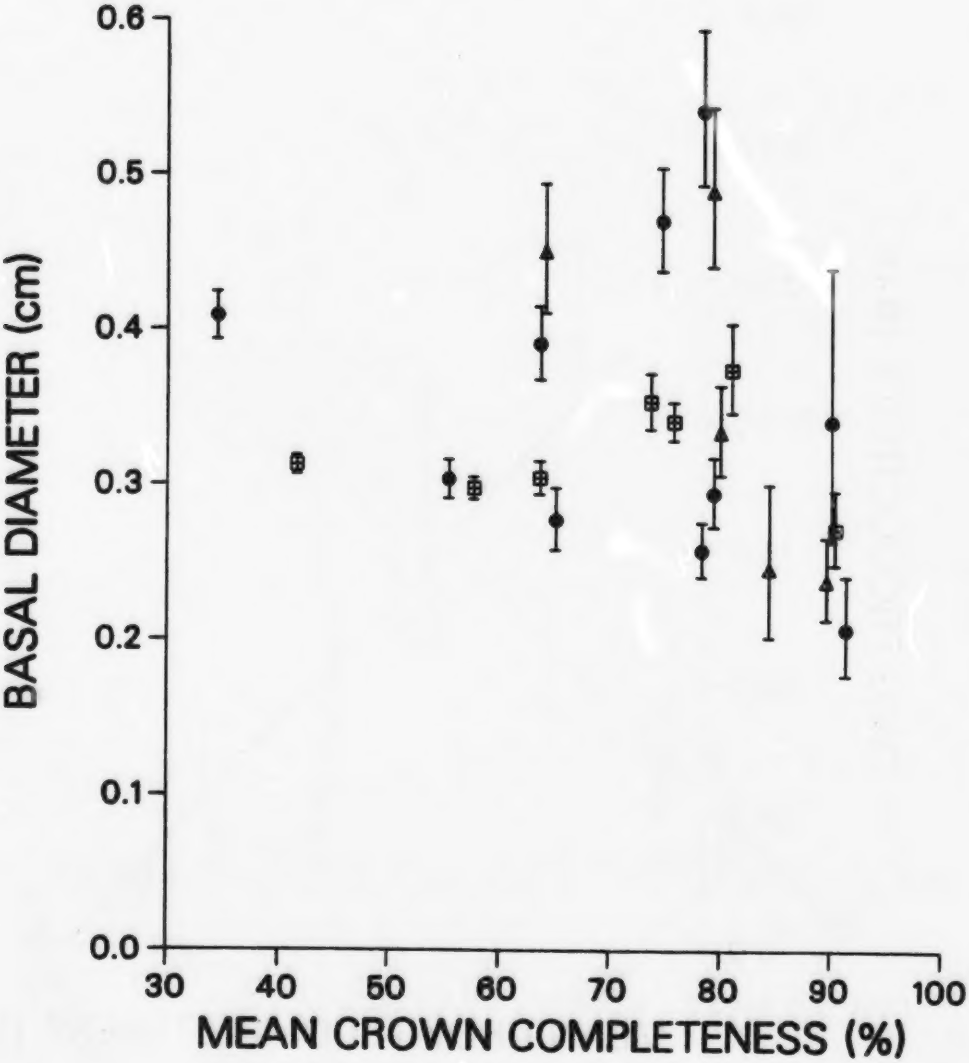
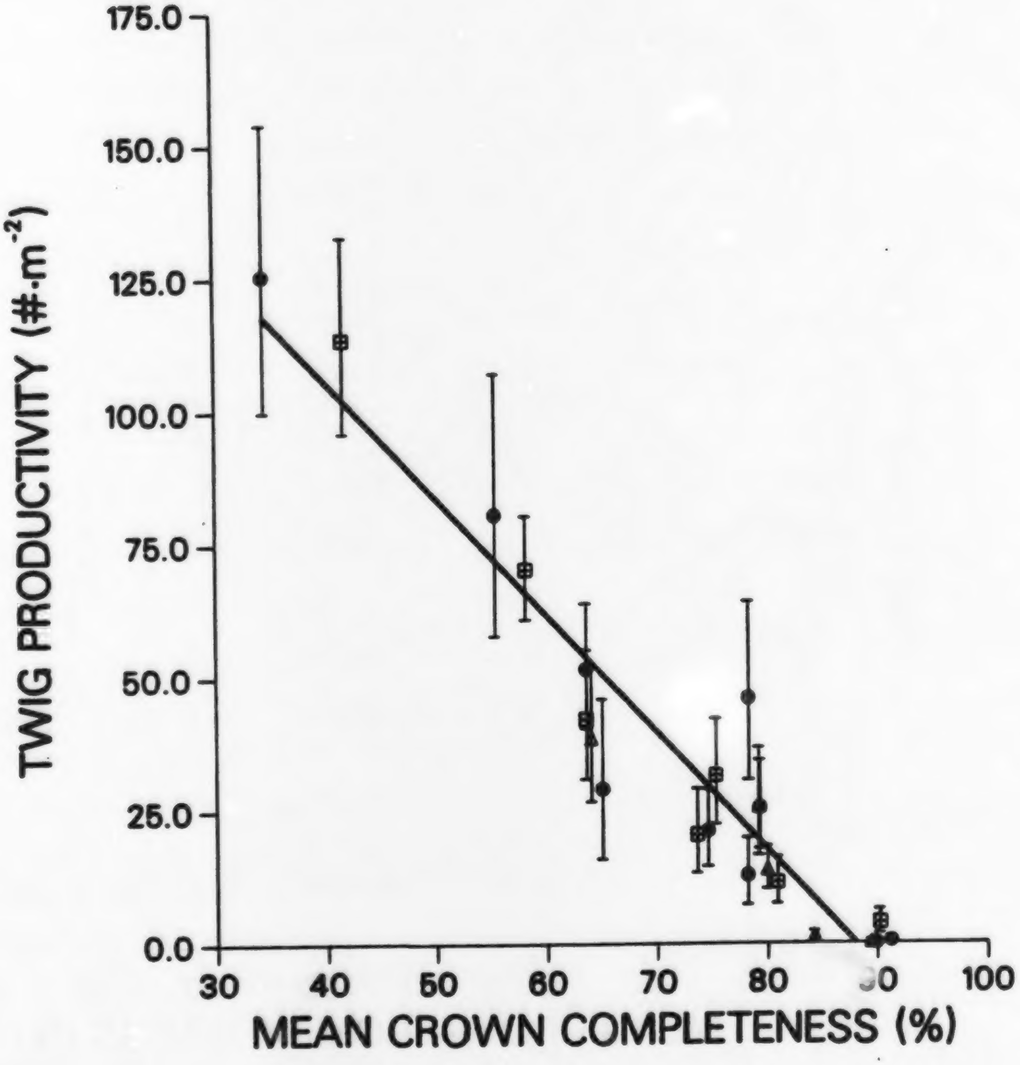
[a] Prefix 1/ refers to the reciprocal of the independent variable.

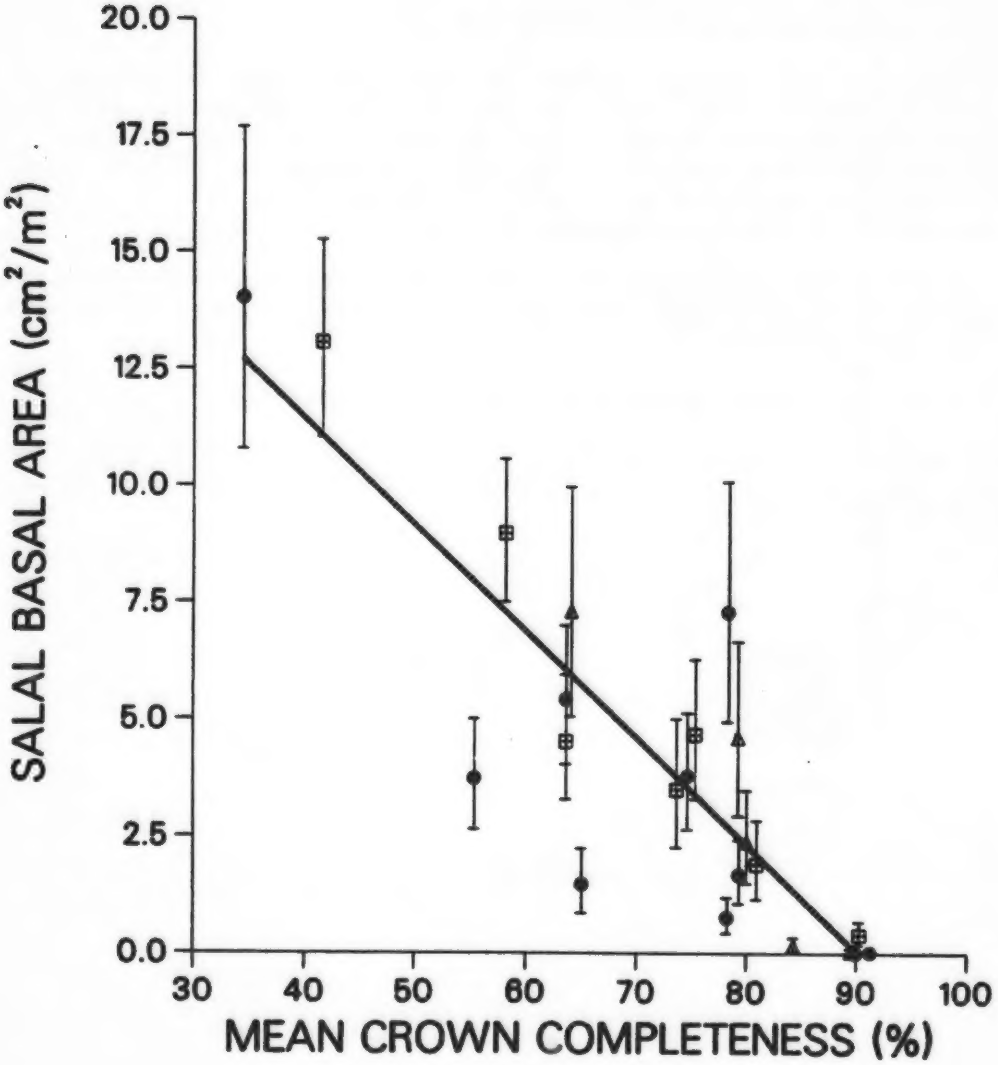
[b] Coefficient not significant ($p \geq 0.10$).



Appendix 10. The relationship of average basal diameter of salal shoots and 95% confidence intervals to mean crown completeness.



Appendix 11. The relationship of twig productivity (# CAG twigs) and 95% confidence intervals to mean crown completeness. Equation: #CAGtwigs·m^{-2} = 193.81 − 219.93·MCC r^2=0.91, $s_{y\cdot x}$=10.7.



Appendix 12. The relationship of salal basal area (cm²/m²) and 95% confidence intervals to mean crown completeness. Equation: Basal area = 20.57 - 22.80·MCC r^2=0.76, $s_{y \cdot x}$=2.0.

APPENDIX 13

The relationship of salal shoot posture to mean crown completeness

The relationship between salal shoot posture and overstory cover was investigated. An average plot index of posture termed "flimsiness index" (FI) was derived from shoot heights by:

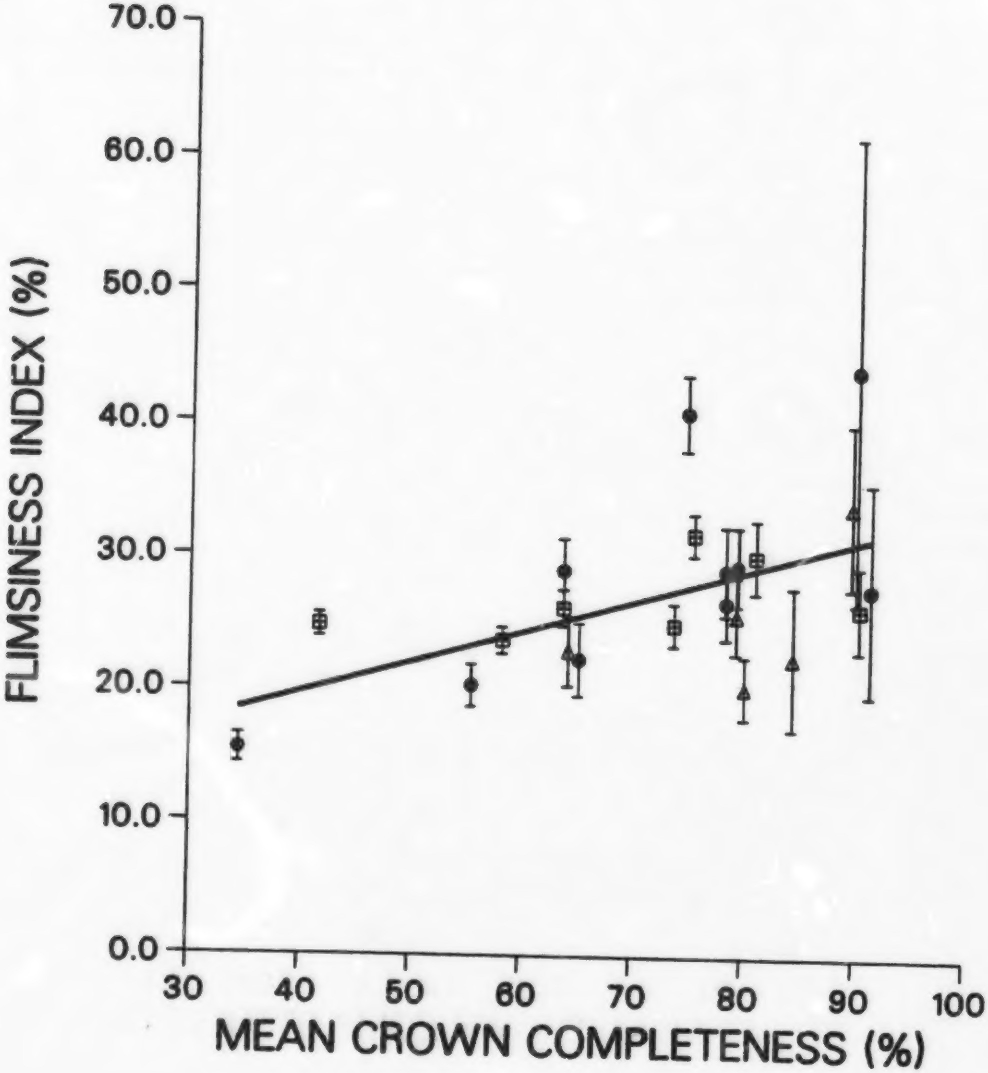
$$FI = (\Sigma((STRETCH-REPOSE)/STRETCH)/n) \cdot 100$$

FI indicates the average percent of each shoot that is reduced from the potential maximum shoot repose height (FI = 0 if all shoots in a plot have repose height=stretch height). The relationship of FI to MCC is illustrated with 95% confidence intervals (Fig. 13a). Although variable, a significant, positive relationship of potential "flimsiness" to MCC is indicated for combined data (r^2=0.29, $s_{y.x}$=5.6%, $p < 0.01$).

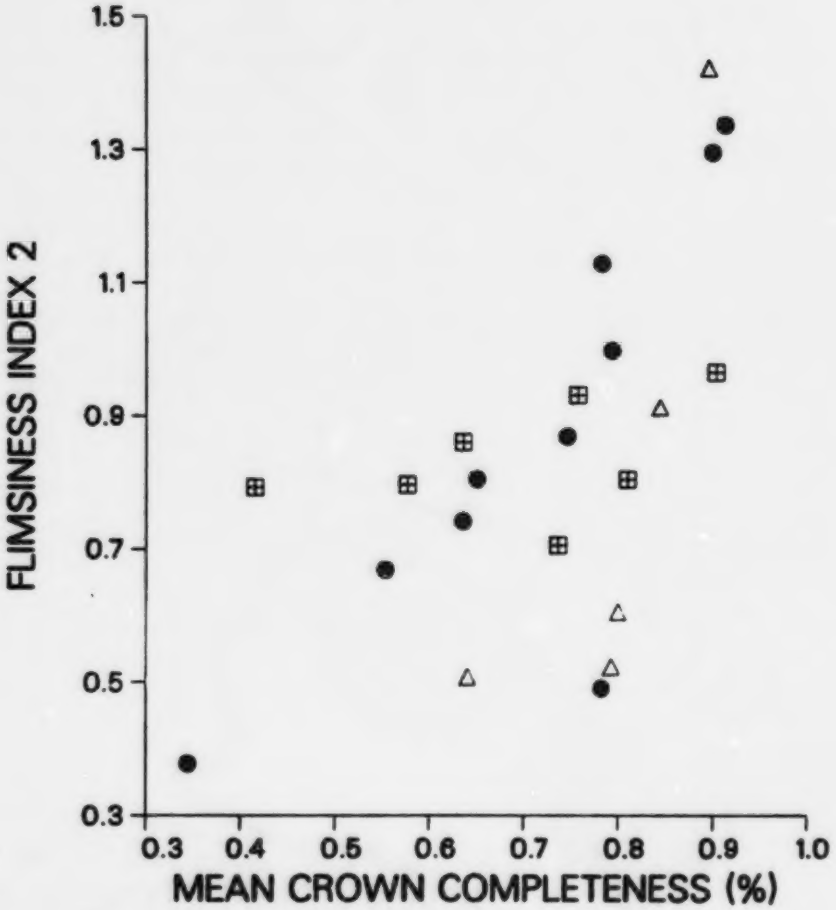
A second index accounting for shoot size was also calculated and the relationship to overstory cover noted. This index, termed "flimsiness index 2" was developed from:

$$FI\ 2 = \Sigma((STRETCH-REPOSE)/STRETCH/\text{Basal diameter})/n$$

FI 2 was strongly related to MCC (Fig. 13b), indicating that under increasing MCC, shoots were increasingly reduced from potential maximum repose height per unit basal diameter.



Appendix 13a. The relationship of salal shoot posture (flimsiness index) and 95% confidence intervals to mean crown completeness.



Appendix 13b. The relationship of salal shoot posture (flimsiness index 2) to mean crown completeness.

APPENDIX 14 Distribution of repose heights of salal shoots by plot. Distribution is percent of shoot density in each height class

	Repose height class (cm)						
Plot	0-19	20-39	40-59	60-79	80-99	100-119	120+
1	67.3	26.1	6.5	0.	0.	0.	0.
2	51.4	21.9	9.3	2.4	1.0	0.	0.
3	58.4	26.1	12.1	3.5	0.	0.	0.
4	53.9	27.5	13.5	3.3	1.6	0.	0.
5	38.2	32.7	15.6	8.3	3.8	1.3	0.9
6	20.8	19.2	19.6	16.0	10.0	8.4	6.4
7	32.7	27.6	19.5	10.1	6.1	2.3	1.5
8	55.7	26.2	11.4	4.4	1.8	0.4	0.
9	61.6	38.5	0.	0.	0.	0.	0.
10	30.3	42.2	16.3	6.8	4.0	0.4	0.4
11	68.2	31.9	0.	0.	0.	0.	0.
12	34.0	16.6	14.2	9.3	10.4	5.4	9.8
13	40.0	29.7	14.6	7.9	2.2	1.2	3.9
14	60.8	25.1	9.0	3.6	0.	0.	1.8
15	24.0	15.1	15.2	15.7	13.1	5.2	11.2
21	55.6	33.4	8.8	1.8	0.3	0.	0.1
22	66.3	29.1	4.3	0.4	0.	0.	0.
23	43.8	27.8	13.9	8.8	3.4	0.9	1.2
24	50.5	36.2	10.0	2.9	0.2	0.1	0.1
25	40.0	34.3	15.5	6.2	2.2	1.1	0.4
26	67.2	24.0	7.6	1.4	0.	0.	0.
27	35.0	42.2	15.4	4.1	2.4	0.6	0.6

APPENDIX 15 Percent frequency of occurrence of species found in quadrats

Species	Plot number																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	21	22	23	24	25	26	27
Gaultheria shallon	21.2	76.9	96.2	88.5	98.1	94.2	99.9	80.8	13.5	96.2	32.7	96.2	92.3	62.3	92.3	99.9	98.1	84.6	94.2	82.7	59.6	86.5
Vaccinium parvifolium	32.7	84.6	30.8	51.9	3.8	19.2	40.4	13.5	15.4	11.5	40.4	11.5	1.9	9.6		53.8	88.5	59.6	32.7	5.8	19.2	63.5
Mahonia nervosa		19.2	21.2	15.4	36.5	46.2			21.2	13.5		46.2	17.3	28.8	61.5	17.3	3.8	1.9	19.2	21.2		1.9
Rubus ursinus		23.1	59.6	13.5	5.8	7.7			1.9	26.9		3.8	1.9		1.9	21.2	23.1	7.7	3.8	1.9		1.9
Tsuga heterophylla	36.5	3.8	1.9	3.8		1.9	11.5	19.2	11.5		1.9	5.8	5.8	7.7	3.8	7.7	1.9	13.5	7.7	13.5	15.4	15.4
Pseudotsuga menziesii	1.9	1.9	3.8	9.6		3.8	7.7			3.8			1.9	5.8	3.8	9.6	1.9	5.8	1.9	5.8	1.9	11.5
Thuja plicata		7.7	1.9	1.9				3.8				11.5	1.9					1.9	5.8	3.8	9.6	1.9
Chimaphila spp.		3.8		1.9	9.6	5.8			5.8	42.3					1.9			1.9	1.9			
Goodyera oblongifolia		7.7																				
Linnaea borealis		1.9			3.8									1.9		34.6	3.8		9.6	1.9		15.4
Gramineae spp.			1.9	1.9						3.8						9.6	1.9	1.9				
Hieracium albiflorum			7.7													21.2	32.7		3.8	1.9		1.9
Fragaria spp.			7.7																			
Agoseris spp.			1.9																			
Maianthemum dilatatum			1.9							1.9												
Equisetum spp.			1.9																			
Polystichum munitum				1.9					1.9			1.9			1.9		3.8	1.9		5.8	5.8	
Lonicera ciliosa				1.9		7.7				40.4												
Viola orbiculata				1.9					5.8	7.7						32.7				1.9		
Trientalis latifolia					7.7					19.2						15.4	11.5					
Achlys triphylla						5.8				65.4						3.8		1.9				1.9
Pteridium aquilinum										36.5			5.8	11.5	1.9					9.6	3.8	
Anaphalis margaritacea																	19.2					
Salix scouleriana																5.8		7.7	9.6	7.7	9.6	5.8
Chamaecyparis nootkatensis																		3.8				
Abies amabilis																		1.9		1.9		5.8
Pinus monticola																			1.9		3.8	1.9
Pyrola spp.									1.9													3.8
Rosa gymnocarpa										13.5						1.9	1.9					
Streptopus streptopoides										3.8												
Amelanchier alnifolia										1.9												
Taxus brevifolia																1.9		1.9			3.8	3.8
Holodiscus discolor																1.9						
Montia spp.																	1.9					
Epilobium angustifolium																	3.8					
Rubus spectabilis																		1.9				

APPENDIX 16 Average quadrat (0.25 m²) density of understory species other than salal

Species	Plot number																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	21	22	23	24	25	26	27
Vaccinium parvifolium	1.60	1.87	1.04	0.89	0.04	0.19	0.40	0.14	0.65	0.12	1.29	0.21	0.10	0.10		0.54	0.88	0.77	0.35	0.15	0.19	0.71
Mahonia nervosa		0.46	0.48	0.31	0.71	0.98			0.35	0.27		1.35	0.33	0.58	1.94	0.54	0.12	0.02	0.48	0.52		0.02
Rubus ursinus		0.50	1.29	0.23	0.06	0.08			0.02	0.38		0.06	0.02		0.02	0.58	0.27	0.15	0.04	0.06		0.04
Tsuga heterophylla	0.42	0.04	0.08	0.04		0.02	0.15	0.27	0.12		0.03	0.06	0.06	0.08	0.04	0.08	0.02	0.13	0.08	0.13	0.15	0.25
Pseudotsuga menziesii	0.02	0.32	0.04	0.10		0.04	0.08			0.04			0.02	0.06	0.04	0.10	0.02	0.06	0.02	0.04	0.02	0.12
Thuja plicata		0.08	0.02	0.06				0.15				0.12	0.03					0.02	0.06	0.04	0.10	0.02
Chimaphila spp.		0.19		0.04	0.27	0.10			0.06	1.43					0.02			0.02	0.02			
Goodyera oblongifolia		0.10																				
Linnaea borealis		0.02			0.04									0.02		1.60	0.08		0.25	0.02		0.68
Gramineae spp.			0.15	0.04						0.13						0.15	0.02	0.02				
Hieracium albiflorum			0.23													0.58	1.17		0.06	0.17		0.02
Fragaria spp.			0.19																			
Agoseris spp.			0.04																			
Maianthemum dilatatum			0.10							0.06												
Equisetum spp.			0.02																			
Polystichum munitum				0.02					0.04			0.02			0.02		0.04	0.02		0.08	0.08	
Lonicera ciliosa				0.04		0.14				1.40												
Viola orbiculata				0.04					0.25	0.21						1.69				0.02		
Trientalis latifolia					0.25					0.48						0.54	0.42					
Achlys triphylla						0.06				2.23						0.10		0.02				0.04
Pteridium aquilinum										0.58			0.06	0.12	0.04					0.10	0.04	
Anaphalis margaritacea																	0.56					
Salix scouleriana																0.08		0.08	0.10	0.08	0.13	0.08
Chamaecyparis nootkatensis																		0.04				
Abies amabilis																		0.02		0.02		0.06
Pinus monticola																			0.02		0.04	0.02
Pyrola spp									0.03													0.17
Rosa gymnocarpa										0.19						0.04	0.04					
Streptopus streptopoides										0.13												
Ammelanchier alnifolia										0.02												
Taxus brevifolia																0.02		0.02			0.06	0.04
Holodiscus discolor																0.02						
Montia perfoliata																	0.08					
Epilobium angustifolium																	0.04					
Rubus spectabilis																		0.02				

APPENDIX 17 List of cover classes for species present in plots[a]

Species	Plot number																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	21	22	23	24	25	26	27
TREES:																						
Abies amabilis																		+	1	+	1	1
Alnus rubra									1										+			
Chamaecyparis nootkatensis																		2		1	+	1
Pinus monticola		+		+									+	+			+	+	2		1	1
Pseudotsuga menziesii	3	5	2	4	5	5	3	3	3	4		4	5	4	4	4	4	3	3	3	2	3
Taxus brevifolia																+	+	+	+	+	+	+
Thuja plicata	+	2	+	+				3	1		4	2	2	1	2			2	2	1	1	1
Tsuga heterophylla	5	4	+	2		+	2	2	4	1	3	1	3	2	2	2	2	3	2	2	5	3
SHRUBS and FERNS:																						
Amelanchier alnifolia			+							1												
Chimaphila spp.	1	+		+	+	+			1	1					+			+	+			
Cladothamnus pyroliflorus											+											
Equisetum spp.			+																			
Gaultheria shallon	1	3	4	4	5	4	4	4	2	5	1	5	4	1	3	5	5	3	4	3	2	3
Holodiscus discolor																+						
Linnaea borealis		+	+		+	+								+		2	+		1	+		+
Lonicera ciliosa				+		+				1												
Lycopodium spp.	+																		+			
Mahonia nervosa		2	2	2	2	2		2	2	2		2	1	1	2	2	1	+	1	1		1
Polystichum munitum	2	1	+	2	1	+			+			+	1	1	+	1	+	+	+	+	+	+
Pteridium aquilinum	1		+	1	+	1	2		+	2			1	1	+			+	+	+	1	1
Rosa gymnocarpa			+		+	+				1						+	+					+
Rubus spectabilis		+																+				
Rubus ursinus		2	2	1	+	+		2	+	1		+	+		+	1	+	+	+	+	+	+
Salix scouleriana									+							1	2	2	1	+	2	1
Vaccinium ovalifolium			+																	+	+	
Vaccinium parvifolium	2	2	2	2	1	2	2	2	3	2	1	1	1	1	2	2	3	2	2	2	2	2
HERBS:																						
Achlys triphylla		+		+		+			+	2				+		+		+				+
Agoseris spp.			+																			
Anaphalis margaritacea																	1					
Epilobium angustifolium																	+					
Fragaria spp.			+																			
Goodyera oblongifolia		1		+																		
Gramineae spp.			+	+						1						1	+	+				
Hieracium albiflorum		+	1													1	1		+	+		+
Maianthemum dilatatum			+							+												
Montia spp.													+				+					
Orthilia secunda		+																				
Pyrola spp.									+													+
Streptopus streptopoides										+												
Trientalis latifolia					+					1						1	1					
Trillium ovatum										+												
Viola orbiculata		1		+					+	+						1				+		
MOSSES and LICHENS:																						
Cladina spp.			3																			
Dicranum spp.		+	1	2			1		+	+												
[illegible] congestum							1															
Hylocomium splendens	2	3	1	3	1	1	4	2	+												1	
Kindbergia oregana		4	2	4	3	3	2	2	2	+		4	4	2	2	2	2		1	+	1	+
Plagiothecium undulatum	2	1		2	1				+	+	+			1								
Polytrichum juniperinum			1																			
Rhytidiadelphus loreus		1		1	1						+											
Rhytidiadelphus triquetrus						1																

[a] Cover classes sensu Klinka et al. (1984): + = <1%, 1 = 1-<5%, 2 = 5-<25%, 3 = 25-<50%, 4 = 50-<75%, 5 = ≥75%.

APPENDIX 18 Results of site diagnosis

Plot	Hygrotope	Trophotope	Grid No.	Site unit
1	3	B-C	7	4
2	2-3	B-C	7	2
3	2	B	7	2
4	2-3	B-C	7	2
5	3	B-C	7	4
6	3	B-C	7	2
7	2-3	B-C	7	2-4
8	2-3	B-C	7	2
9	2-3	B-C	7	2
10	2-3	B-C	7	2
11	2-3	B	9	2
12	2	B	9	2
13	2-3	B-C	9	2
14	2-3	B-C	9	2
15	2	B	9	2
21	2-3	B-C	11	2
22	2-3	B-C	11	2
23	2-3	B-C	11	2
24	2-3	B-C	11	2
25	2-3	B-C	11	2
26	3	B-C	11	2
27	2-3	B-C	11	2

APPENDIX 19 Regression coefficients of equations predicting solar radiation components from stand characteristics. Sample sizes: CWHa=6, CWHb=6. Equations significant at $p \leq 0.10$. Regression equation: $Y = ae^{-bX}$

Y	Subzone	X	a	b	r^2	$s_{y \cdot x}$
TOTAL:	CWHa	NTREES	1.0716	3.1539E-3[a]	0.89	0.0610
		BA	1.6708	8.6639E-2	0.97	0.0324
		BAFBA	5.8482	0.1381	0.92	0.0485
	CWHb	NTREES	8.0679	3.5850E-3	0.92	0.0624
		BA	1.3098	0.1193	0.84	0.0880
		BAFBA	1.3583	0.1097	0.93	0.0579
	Both	NTREES	0.6640	1.1225E-3	0.63	0.1143
		BA	0.8840	7.2005E-2	0.79	0.0850
		BAFBA	1.0616	7.9569E-2	0.77	0.0895
DIFFUSE:	CWHa	NTREES	0.7272	5.0976E-4	0.58	0.1527
		BA	1.2563	3.7167E-2	0.68	0.1339
		BAFBA	N.S.[b]		0.48	0.1709
	CWHb	NTREES	3.0165	7.5458E-4	0.93	0.1598
		BA	2.3034	3.5136E-2	0.89	0.2013
		BAFBA	2.6304	4.3310E-2	0.80	0.2727
DIRECT:	CWHa	NTREES	1.3409	4.2749E-3	0.95	0.0394
		BA	2.1132	0.1078	0.98	0.0247
		BAFBA	11.2441	0.1777	0.96	0.0353
	CWHb	NTREES	230.5546	8.3632E-3	0.99	0.0204
		BA	213.0794	0.7341	0.98	0.0263
		BAFBA	9.3088	0.3536	0.98	0.0247
	Both	NTREES	0.7036	1.7435E-3	0.69	0.0885
		BA	0.7069	8.5952E-2	0.59	0.1031
		BAFBA	0.8231	9.0618E-2	0.55	0.1070
PAR:	CWHa	NTREES	0.4157	1.6161E-3	0.86	0.0430
		BA	0.8569	7.4090E-2	0.95	0.0264
		BAFBA	2.2549	0.1131	0.88	0.0396
	CWHb	NTREES	0.8099	1.5746E-3	0.88	0.0380
		BA	0.4242	6.7017E-2	0.85	0.0419
		BAFBA	0.4800	7.1875E-2	0.83	0.0449
	Both	NTREES	0.3845	1.0378E-3	0.75	0.0515
		BA	0.4213	5.6009E-2	0.78	0.0481
		BAFBA	0.4691	6.1045E-2	0.68	0.0579

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[a] Exponent for power of 10.

[b] Equation not significant ($p > 0.10$).

APPENDIX 20 Regression coefficients of equations predicting solar radiation components from stand characteristics. Sample sizes: CWHa=6, CWHb=6. Equations significant at $p \leq 0.05$. Regression equation: $Y = e^{-bX}$

Y	Subzone	X	b	r^2	$s_{y \cdot x}$
TOTAL:	CWHa	MCC	2.9899	0.85	0.0713
		SUMDIA	5.5965E-3[a]	0.95	0.0414
		SDI	2.8797E-3	0.95	0.0396
		BAFSDI	2.7659E-3	0.70	0.1028
	CWHb	MCC	2.3816	0.69	0.1232
		SUMDIA	4.4934E-4	0.80	0.0983
		SDI	3.5185E-3	0.84	0.0878
		BAFSDI	3.2876E-3	0.91	0.0663
	Both	MCC	2.6362	0.73	0.0974
		SUMDIA	4.8113E-4	0.85	0.0725
		SDI	3.2665E-3	0.87	0.0665
		BAFSDI	3.0606E-3	0.81	0.0817
DIFFUSE:	CWHa	MCC	1.4802	0.74	0.1217
		SUMDIA	2.0949E-4	0.71	0.1280
		SDI	1.3024E-3	0.69	0.1310
		BAFSDI	N.S.[b]		
	CWHb	MCC	N.S.		
		SUMDIA	N.S.		
		SDI	N.S.		
		BAFSDI	N.S.		
DIRECT:	CWHa	MCC	3.2988	0.84	0.0731
		SUMDIA	6.4419E-4	0.98	0.0284
		SDI	3.2266E-3	0.95	0.0389
		BAFSDI	3.0370E-3	0.68	0.1015
	CWHb	MCC	3.2984	0.66	0.1032
		SUMDIA	6.6399E-4	0.70	0.0970
		SDI	5.3104E-3	0.77	0.0851
		BAFSDI	4.8240E-3	0.86	0.0659
	Both	MCC	3.2985	0.75	0.0800
		SUMDIA	6.5725E-4	0.84	0.0829
		SDI	4.4815E-3	0.73	0.0975
		BAFSDI	4.0347E-3	0.63	0.0731
PAR:	CWHa	MCC	3.7696	0.95	0.0270
		SUMDIA	8.9596E-4	0.79	0.0526
		SDI	3.9498E-3	0.91	0.0346
		BAFSDI	3.3928E-3	0.86	0.0426
	CWHb	MCC	3.2611	0.67	0.0636
		SUMDIA	6.6389E-4	0.88	0.0378
		SDI	5.4516E-3	0.74	0.0564
		BAFSDI	4.9271E-3	0.65	0.0648
	Both	MCC	3.4824	0.79	0.0473
		SUMDIA	7.3004E-4	0.77	0.0496
		SDI	4.9477E-3	0.74	0.0521
		BAFSDI	4.2759E-3	0.60	0.0649

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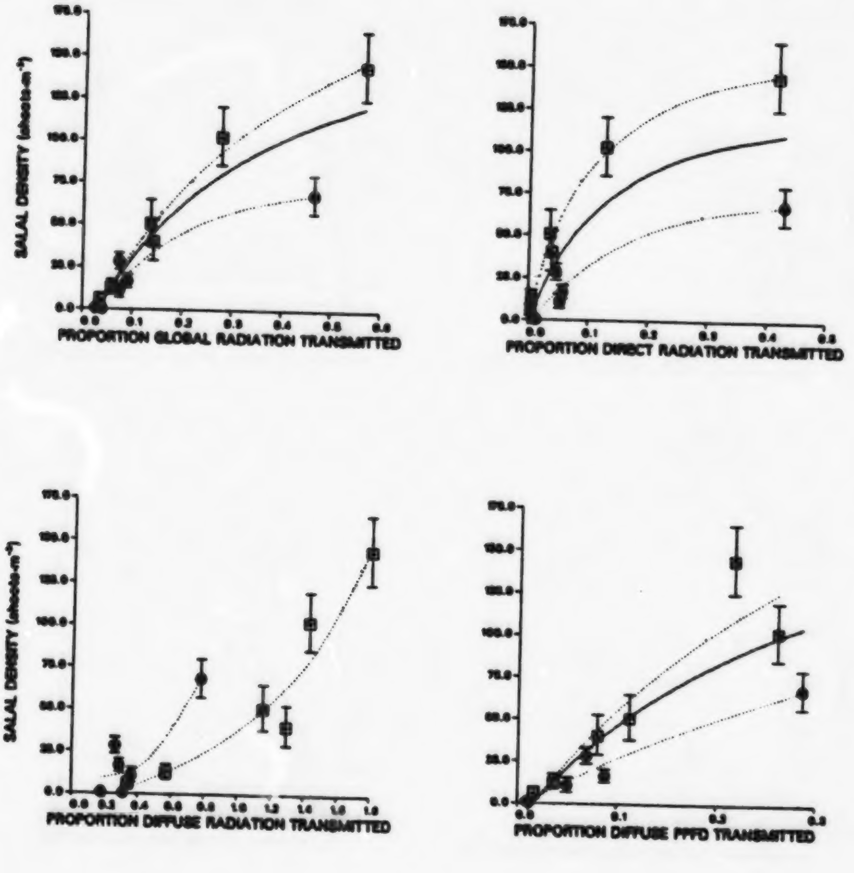
[a] Exponent for power of 10.

[b] Equation not significant ($p > 0.05$).

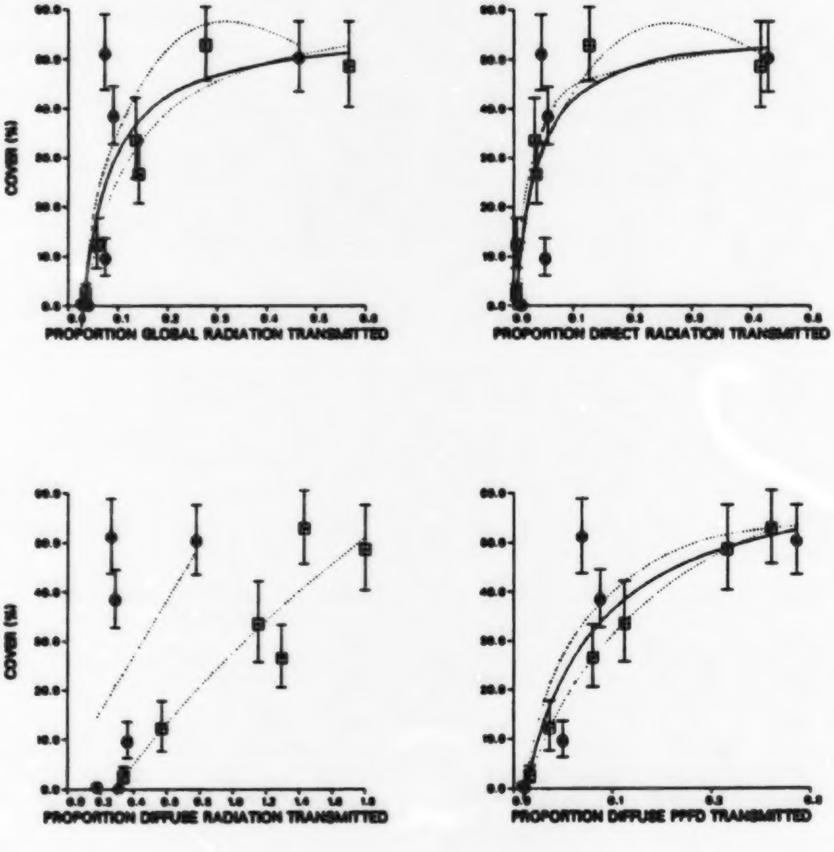
APPENDIX 21 Regression coefficients of equations predicting salal from site factors derived from hemispherical photographs. Sample sizes: CWHa=5, CWHb=6.

Regression equation: $Y = \frac{a(X-c)}{1 + a(X-c)/b}$

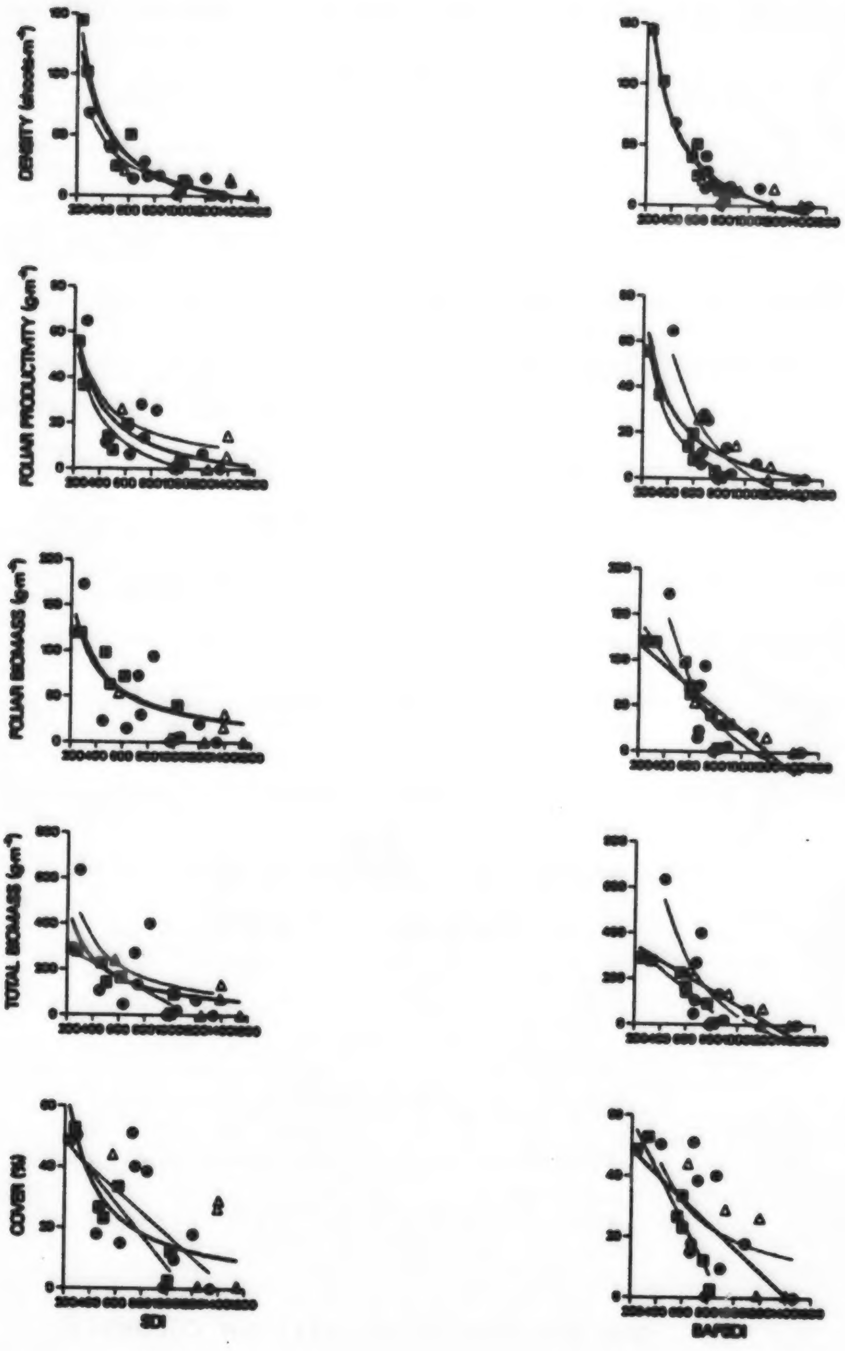
Y	Subzone	X	a	b	c	r^2	$s_{y\cdot x}$	p
DENSITY:	CWHa	DIFFUSE SF	844.3	105.8	0.0920	0.96	5.7	<0.01
		DIRECT SF	3.3	-2.5	-0.4638	0.86	11.4	<0.05
	CWHb	DIFFUSE SF	707.9	46781946	0.0711	0.92	17.0	<0.01
		DIRECT SF	1127.5	83915.0	0.0889	0.55	40.5	0.09
	Both	DIFFUSE SF	992.5	208.8	0.0826	0.70	26.0	<0.01
		DIRECT SF	587.6	225.2	0.0653	0.13	44.5	0.27
SALALBA:	CWHa	DIFFUSE SF	173.8	21.4	0.0879	0.78	3.1	<0.05
		DIRECT SF	106.7	11327.4	0.1326	0.76	3.2	0.06
	CWHb	DIFFUSE SF	60.5	19180.0	0.0623	0.89	1.7	<0.01
		DIRECT SF	94.2	12179.0	0.0821	0.51	3.7	0.11
	Both	DIFFUSE SF	77.4	52.9	0.0674	0.82	2.2	<0.01
		DIRECT SF	75.4	14928.8	0.0872	0.47	3.7	<0.05
TOTBIOM:	CWHa	DIFFUSE SF	9560.0	879.8	0.0881	0.68	174.8	0.09
		DIRECT SF	2994.0	-1252.3	0.1166	0.70	168.3	0.08
	CWHb	DIFFUSE SF	5572.0	383.5	0.0689	0.79	56.3	<0.05
		DIRECT SF						0.90
	Both	DIFFUSE SF	1854.3	321152.0	0.0372	0.57	131.9	<0.01
		DIRECT SF	3133.5	476216.0	0.0917	0.53	138.4	<0.05
CAGBIOM:	CWHa	DIFFUSE SF	787.9	101.0	0.0906	0.84	12.0	<0.05
		DIRECT SF	29.6	-9.4	-0.0209	0.78	14.3	<0.05
	CWHb	DIFFUSE SF	273.6	50096.0	0.0759	0.90	7.3	<0.01
		DIRECT SF	431.9	8475943	0.0916	0.53	16.1	0.10
	Both	DIFFUSE SF	299.9	501.3	0.0718	0.85	9.1	<0.01
		DIRECT SF	356.6	71767.0	0.0972	0.51	16.5	<0.05
PCTCOVER:	CWHa	DIFFUSE SF	3183.0	54.7	0.0922	0.61	17.1	0.12
		DIRECT SF	279.9	2468.1	0.0757	0.28	23.0	0.36
	CWHb	DIFFUSE SF	581.8	100.2	0.0671	0.93	6.0	<0.01
		DIRECT SF	322.2	70208.0	0.0501	0.33	18.0	0.23
	Both	DIFFUSE SF	941.1	71.2	0.0730	0.67	12.4	<0.01
		DIRECT SF	223.7	20414.0	0.0281	0.24	18.9	0.13



Appendix 22. Relationships of salal density (#·m⁻²) and 95% confidence intervals to transmission of global, direct, diffuse, and diffuse PPFD solar radiation components. Dotted lines are relationships in individual subzones. CWHa (●), CWHb (⊞).



Appendix 23. Relationships of percent cover of salal and 95% confidence intervals to transmission of global, direct, diffuse, and diffuse PPFD solar radiation components. Dotted lines are relationships in individual subzones. CWHa (•), CWHb (⊞).



Appendix 24. Relationships of salal DENSITY, CAGBIOM, FOLBIOM, TOTBIOM, and PCTCOVER to Reineke's SDI derived from plot tree measurements (SDI) and prism samples (BAFSDI). Dotted lines are separate relationships in CWHa and CWHb, variants.

FUNCTIONAL RELATIONSHIPS BETWEEN SALAL UNDERSTORY AND FOREST OVERSTORY

By

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B.Sc., Iowa State University, 1981

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(Faculty of Forestry)

We accept this thesis as conforming
to the required standard

....
J.H.G. Smith
Michael I. Pitt
J. Brian Nyberg

THE UNIVERSITY OF BRITISH COLUMBIA

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